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Principal predators and consumption of juvenile and adult Atlantic Herring (*Clupea harengus*) in the southern Gulf of St. Lawrence

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Herring (*Clupea harengus*) is a key prey species in the diets of numerous fishes, marine mammals, seabirds, and large pelagic predators in many North Atlantic ecosystems, including the southern Gulf of St. Lawrence (sGSL; NW Atlantic, Canada). Like many small pelagic forage fish species, predation can be a significant source of mortality in Herring, rivaling or exceeding fishery removals. Changes in the abundance of Herring and their predators can therefore lead to important non-stationarity in Herring productivity, which, if unaccounted for, can bias the perception of stock status and its response to given levels of fishing. In this report we review the available information on interannual and seasonal trends in the abundance, distribution and diet of the major predators of Herring in the sGSL. This information was assembled in support of an assessment framework review for sGSL fall-spawning Herring that took place on April 13-15, 2015. Sufficient information was available to estimate the annual consumption of sGSL Herring by Northern Gannets (*Morus bassanus*), Cormorants (*Phalacrocorax* sp.), Grey Seals (*Halichoerus grypus*), Bluefin Tuna (*Thunnus thynnus*), White Hake (*Urophycis tenuis)* and Atlantic Cod (*Gadus morhua*). The reliability of those estimates varied between predators and was best for the groundfish predators. Consumption by cetacean predators could only be estimated for the mid-1990s, where it represented 37% of total estimated consumption by predators, indicating that consumption estimates for other years could be significantly biased low. For 2013, consumption by all predators other than cetaceans was almost equal to landings in the fishery, confirming the relative importance of natural mortality for this forage fish. Consumption of Herring by Cod, a historically important predator, peaked in the mid-1980s and has been declining since then. The declines since 1990 in consumption by Cod and White Hake have been offset by estimated increases in consumption by Grey Seals and Northern Gannets. The amount of Herring consumed annually by Bluefin Tuna is somewhat uncertain, but is likely to have increased to a relatively important level since 2000. Additional abundance surveys for certain key predators (e.g., cetaceans, Bluefin Tuna) and ongoing monitoring of predator diets will improve consumption estimation, ideally eventually to a point where this information can be more directly incorporated in the assessment of sGSL Herring. For now, the available information is most useful for identifying key predators, changes over time in their relative importance and an indication of the overall scale of predation mortality for sGSL Herring.

Principaux prédateurs et consommation de harengs de l'Atlantique (*Clupea harengus*) juvéniles et adultes dans le sud du golfe du Saint-Laurent

RÉSUMÉ

Le hareng (*Clupea harengus*) est l'une des principales espèces de proies de plusieurs poissons, mammifères marins, oiseaux de mer et grands prédateurs pélagiques dans de nombreux écosystèmes de l'Atlantique Nord, y compris le sud du Golfe du Saint-Laurent (sGSL; Atlantique Nord-Ouest, Canada). Comme pour bien des petites espèces de poissons fourrages pélagiques, la prédation peut représenter une importante source de mortalité pour le hareng, égale aux prélèvements par la pêche, si ce n'est pire que celle-ci. Les changements dans l'abondance du hareng et de leurs prédateurs peuvent donc entraîner un manque important de stationnarité de la productivité du hareng, ce qui peut fausser la perception de l'état du stock et de sa réaction à des niveaux de pêche donnés. Dans le présent rapport, nous avons examiné les renseignements disponibles sur les tendances interannuelles et saisonnières de l'abondance, de la répartition et du régime alimentaire des principaux prédateurs du hareng dans le sGSL. Cette information a été recueillie à l'appui d'un examen du cadre d'évaluation pour la composante de reproducteurs d'automne du sGSL qui a été mené du 13 au 15 avril 2015. Les renseignements étaient suffisants pour estimer la consommation annuelle de harengs du sGSL par le fou de Bassan (*Morus bassanus*), le cormoran (*Phalacrocorax* sp.), le phoque gris (*Halichoerus grypus*), le thon rouge (*Thunnus thynnus*), la merluche blanche (*Urophycis tenuis)* et la morue franche (*Gadus morhua*). La fiabilité de ces estimations variait selon les prédateurs et était meilleure pour les prédateurs des poissons de fond. La consommation par des cétacés n'a pu être estimée que pour le milieu des années 1990, où elle représentait 37 % de la consommation totale estimée par des prédateurs, ce qui indique que les estimations de la consommation pour les autres années pourraient être considérablement biaisées à la baisse. En 2013, la consommation par tous les prédateurs autres que les cétacés était presque égale aux débarquements de la pêche, confirmant ainsi l'importance relative du taux de mortalité naturelle de cette espèce fourragère. La consommation de hareng par la morue, un prédateur important par le passé, a atteint un sommet au milieu des années 1980, mais affiche une baisse depuis. Le déclin observé depuis 1990 dans la consommation par la morue et la merluche blanche a été compensé par des augmentations estimées de la consommation par les phoques gris et les fous de Bassan. La quantité de harengs consommée chaque année par le thon rouge est quelque peu incertaine, mais elle a probablement augmenté à un niveau relativement élevé depuis 2000. Des relevés d'abondance supplémentaires pour certains prédateurs importants (p. ex., cétacés, thon rouge) et la surveillance continue des régimes alimentaires des prédateurs permettront d'améliorer l'estimation de la consommation par les prédateurs, idéalement à un point où ces renseignements pourront être plus directement intégrés au cadre d'évaluation du hareng du sGSL. Pour l'instant, les renseignements disponibles servent surtout à identifier les principaux prédateurs, à définir les changements de leur importance relative au fil du temps et à obtenir une indication de l'échelle globale de la mortalité par prédation du hareng du sGSL.

1. INTRODUCTION

Herring (Clupea harengus) are a key prey species in the diets of numerous fishes, marine mammals, seabirds, and large pelagic predators in many North Atlantic ecosystems (Overholtz et al. 2000; Guenette and Stephenson 2012; Engelhard et al. 2014). This is certainly true for the Atlantic Herring of the southern Gulf of St. Lawrence (sGSL; Fig. 1) (Fontaine et al. 1994; Hanson and Chouinard 2002; Pleizier et al. 2012). As for many small pelagic forage fish species, predation can be a significant source of mortality in Herring, rivaling or exceeding fishery removals (Overholtz and Link 2007). Changes in the abundance of Herring and their predators can therefore lead to important non-stationarity in Herring productivity, which if unaccounted for can bias perception of stock status and its response to given levels of fishing. This situation may apply to fall spawning sGSL Herring (NAFO Div. 4T), for which the most recent assessment model presented important residual and retrospective patterns (LeBlanc et al. 2015). These patterns are consistent with non-stationarity in one or more parameters that were assumed to be temporally invariable, such as natural mortality or catchabilities.

Here we review the available information on interannual and seasonal trends in the abundance, distribution and diet of the major predators of Herring in the sGSL. The focus is on predators of late juvenile and adult Herring, which are the stages that are considered in the assessments for the spring and fall spawning stocks. The objective is to use the best available science to estimate the trends in the consumption of sGSL Herring by predators for the period covered by the assessment, 1978 to 2014. All of the predators considered consume both spring and fall spawning Herring, and it was not possible to estimate consumption specific to each spawning stock. We begin by reviewing the available information for individual predators and estimating contemporary levels of Herring consumption for each. We then combine the available information to estimate a time series of overall consumption.

2. MAJOR PREDATORS: ABUNDANCE, DISTRIBUTION AND CONSUMPTION OF HERRING

2.1 SEABIRDS

Seabirds are estimated to consume around 0.26 tonnes per km^2 of food per year in the Gulf of St. Lawrence and Scotian Shelf (Barrett et al. 2006). For the sGSL this represents around 20,000 tonnes annually. Among the seabirds of the sGSL, Northern Gannets (*Morus bassanus*), Double-crested Cormorants (*Phalacrocorax auritus*) and Great Cormorants (*P. carbo*) are the main consumers of late juvenile and adult Herring (Cairns et al. 1991).

2.1.1 Northern Gannet

2.1.1.1 Abundance and distribution

The Northern Gannet population of the Gulf of St. Lawrence is distributed among three colonies: Bonaventure Island (Gaspé peninsula), Bird Rocks (Magdalen Islands) and Falaise aux Goélands (Anticosti Island). The colony at Bonaventure Island is currently one of the largest in the world, with an estimated 50,608 breeding pairs in 2014 (Murray et al. 2014; Fig. 2). In contrast, the colony on Anticosti Island comprised 165 pairs in 2014. The number of breeding pairs at the two principal colonies increased almost threefold from the 1970s to the early 2000s and has fluctuated at a high level since then (Fig. 2). The total Gulf of St. Lawrence population has not been this large since before 1860 (reviewed in Rail et al. 2013). For example, around 3,500 pairs were reported on Bonaventure Island in 1898 and 1,500 pairs on Bird Rocks in 1904

(Fisher and Vevers 1943). Furthermore, the small colony on Anticosti Island likely wasn't established until the 1910s.

Breeding Northern Gannets occur in the Gulf of St. Lawrence generally from the beginning of April to mid-October (approximately 200 days residence time). The residence time of non-breeding birds is shorter (approximately 150 days; Montevecchi et al. 1988). The foraging areas of gannets at Bonaventure Island have been examined using satellite telemetry of tagged birds conducted in late August 2003 and in June and July 2014 (Garthe et al. 2007; S. Garthe, personal communication to J.-F. Rail). During the first half of June, almost all trips were concentrated in the southwestern Gulf of St. Lawrence. In July and August approximately three-quarter of the trips were made to the southwestern Gulf, with the remainder in the northern Gulf.

2.1.1.2 Diet and consumption of Herring

Comprehensive sampling of Northern Gannet diets on Bonaventure Island based on regurgitations was undertaken from July to early September in 2004 and 2005. Atlantic Mackerel were the principal prey consumed, though Clupeids (likely mainly Atlantic Herring) comprised 45% by weight of the diet in 2004 and 28% in 2005 (Rail et al. 2013). Seasonally limited sampling in other years yielded a percentage of Herring in diets ranging from 10-92% (Rail et al. 2013). For colonies in the sGSL and in Newfoundland, Atlantic Herring appear to be an important component of the diet before July and again after mid-August (Lafleur 1969, cited in Rail et al. 2013; Montevecchi et al. 1988), consistent with Gannets targeting spawning aggregations. The size of Herring observed in small samples of undigested whole fish recovered from regurgitations collected in sGSL colonies ranged from 14 to 33 cm, with a mean of around 28cm (J.-F. Rail, unpublished data).

Montevecchi et al. (1988) estimated that breeding Northern Gannets have a daily energy intake of 6,700 kJ per day. Assuming a prey energy density of 7.56 kJ per g for Herring and 9.44 kJ per g for remaining prey based on Mackerel (Beck et al. 2007), and a seasonally-averaged diet comprised of 35% of Herring (by weight), this results in an estimated consumption of 268 g of Herring per day on average. Given a residence time of 200 days in the Gulf of St. Lawrence and assuming that a seasonal average of 80% of foraging trips are made in the sGSL, the average breeder is estimated to consume about 42.9 kg of Herring per season. Montevecchi et al. (1988) assumed that nonbreeding gannets had an energy intake that was 90% that of breeders. Assuming the same diet and foraging patterns as breeders and a 150 day residence time in the Gulf results in an estimated average seasonal consumption of 28.9 kg of Herring per season for non-breeders. Given the number of breeding gannets, and assuming that the abundance of non-breeders is 25% that of breeders (Montevecchi et al. 1988), we estimate that an average of 8,093 tonnes of sGSL Herring were consumed by Northern Gannets annually during 2005 to 2014.

2.1.2 Cormorants

There are two species of cormorant that reside seasonally in the sGSL; the Double-crested Cormorant (*Phalacrocorax auritus*) and the Great Cormorant (*P. carbo*). Both species are pursuit divers, and individuals from colonies that border the sGSL feed on marine and diadromous fish nearshore, including Herring.

2.1.2.1 Abundance and distribution

There are coastal cormorant colonies in all provinces that border the sGSL. Surveys of breeding pairs or occupied nests for both cormorant species are done sporadically and by different agencies in different provinces. Counts of occupied nests (assumed to be indicative of breeding pair numbers) were obtained from a number of published sources for the following provinces:

Québec (Magdalen Islands and Gaspe Peninsula; Cotter and Rail 2007; Rail 2009; Rail unpublished data), New Brunswick (Davis et al. 2011; note that some surveys did not cover all known colonies) and Nova Scotia (Lock and Ross 1973; Milton and Austin-Smith1983). In all cases, we only used counts for colonies that were along the shores of the sGSL. Data for Prince Edward Island (PEI) were provided by provincial wildlife staff (Brad Potter, pers. comm.), and are the result of complete counts of nests done in a number of years. In 2004 and 2009 there were single colonies in PEI that were not surveyed, and counts for those colonies in adjoining years were used to generate interpolated values.

For each cormorant species we estimated the time series of the number of breeding pairs in each area by fitting a model with areas as factors and a common temporal trend to log-transformed nest (breeding pair) counts. These models assume that the colonies bordering the sGSL may differ in absolute abundance but that they experience similar factors that affect their demographic trends. For *P. auritus*, a linear model provided a good fit to the intra- and inter-colony data, consistent with an exponential increase in the number of pairs breeding along the shores of the sGSL (Fig. 3). For *P. carbo* an additive model with a smoothed temporal term with five degrees of freedom provided an acceptable but not ideal fit to the rather sparse and variable nest count data. The model suggests that abundance increased exponentially from the 1970s to the late 1990s, before declining to levels comparable to those of the early 1990s. Though the suitability of the model for *P. carbo* is uncertain, this species is considerably less numerous than *P. auritus* (Fig. 4) and the consumption by cormorants overall is smaller than that of other Herring predators (described below). Model misspecification for *P.carbo* is therefore unlikely to have important consequences for the estimation of overall Atlantic Herring consumption by predators.

2.1.2.2 Diet and consumption of Herring

Pilon et al. (1983) studied the diets of cormorants on the Magdalen Islands in 1977 and 1978, based on regular sampling of regurgitations covering late spring (1978) and summer (1977 and 1978). Herring represented 13.3% by weight (2.6% by number) of the overall diet of *P. auritus* in 1978, though all Herring were ingested during springtime, near shore. These were presumably spawning Herring. There was no spring sampling of the diet of *P. carbo*, though similarities in the diet of the two cormorant species in other months suggest that the springtime consumption of Herring may be similar. The authors noted that some Herring recovered from diets measured up to 30 cm, weighing up to 185 g. To be useful for the current purposes, the study by Pilon et al. (1983) needs to be placed in the context of the seasonal distribution and abundance of Herring. First, Herring only spawn in the waters near the Magdalen Islands in the spring. It would be reasonable to expect cormorants to have fed on Herring at comparable levels in other times and places when Herring were aggregated to spawn. Second the estimated abundance of spring-spawning sGSL Herring in 1977 to 1978 was estimated at around 85,000 tonnes, which is considerably smaller than the estimated average 350,000 tonnes of fall-spawning Herring for 1985 to the present (LeBlanc et al. 2015). Because cormorants are generalist predators (Cairns 1998), it would therefore be reasonable to assume that their average consumption of Herring for the sGSL could be higher. For example, studies of *P. auritus* diets in the sGSL in the early 1990s reported that Herring comprised around 22% of the diet by number, and occurred in 17% to 21% of samples (Cairns 1998).

The daily energy expenditure (DEE) for cormorants was estimated using the allometric relationship of Birt-Friesen et al. (1989); $DEE = 977\ Mass^{0.727}$ assuming a mean individual mass of 2.3 kg for *P. auritus* and 3.4 kg for *P. carbo* (Cairns et al.1991; Bundy et al. 2000; Cornell Lab of Ornithology). As per Cairns et al. (1991), the DEE was divided by an assimilation efficiency of 0.80 to derive a daily energy requirement of 2,240 kJ per day for *P. auritus* and 2,970 kJ per day for *P. carbo*. Assuming an energy density of 7.56 kJ per g for Herring and 5.3 kJ per g for the

remaining prey which represent a mixture of groundfish and pelagic fish species (Beck et al. 2007), and assuming a recent diet comprised of 20% by weight of Herring, average individual breeding *P. auritus* and *P. carbo* are estimated to consume 78 g and 103 g of sGSL Herring per day respectively.

Cormorants are present in the sGSL from early April until mid-September. Here we assume a 175 day residency period. In contrast to northern gannets, they have a higher fecundity and shorter longevity, resulting in a higher proportion of the population that is composed of non-breeding individuals. Non-breeding individuals born in previous years are estimated to comprise 34% of the population (J.-F. Rail, unpublished data), are assumed to have a similar residency period as breeders, and to have an energy intake that is on average 90% that of breeders (following Montevecchi et al. 1988). Based on these numbers, we estimate that the average breeding individual has a seasonal consumption of 22.7 kg and 30.1 kg of sGSL Herring for *P. auritus* and *P. carbo*, respectively. Based on the estimates of breeding abundances for the sGSL presented above, there is an estimated average of 1,773 tonnes of Herring consumed annually for 2005 to 2014 by cormorants.

2.2 MARINE MAMMALS

2.2.1 Cetaceans

Consumption of Atlantic Herring by whales and dolphins can be considerable. For example, consumption of Gulf of Maine-Georges Bank Herring by cetaceans has been estimated to be elevated and second only to consumption by demersal fish (Read and Brownstein 2003; Overholtz and Link 2007). Unfortunately, there is very limited information available to estimate the possible consumption of Herring by cetaceans in the sGSL. We nonetheless review the available information to derive an estimate for the mid-1990s, which at least provides an estimate of the magnitude of consumption by cetaceans relative to other predators.

2.2.1.1 Abundance

There have only been two systematic aerial surveys of cetaceans in the sGSL, one in 1995-1996 and another in 2007, which were part of the multinational Trans North Atlantic Sightings Survey (TNASS) that extends from the northeastern U.S.A. to the U.K. (Kingsley and Reeves 1998; Lawson and Gosselin 2009). While the 1995 to 1996 survey produced estimates of abundance for certain cetacean species in the sGSL, there are insufficient data to determine the extent to which these estimates could correspond to actual abundance. Estimates for the 2007 survey provided in Lawson and Gosselin (2009) are for an area that is larger than the sGSL (includes the northern Gulf and the Scotian Shelf), and are based on sightings only, in contrast to the 1995 to 1996 estimates for which some attempts were made to scale up observations to abundance estimates. The two surveys are therefore not directly comparable. Nonetheless, the observed raw numbers of each species in 2007 in an area comparable to the area sampled in 1995 to 1996 are summarized here.

Kingsley and Reeves (1998) derived estimates for two strata that cover the sGSL, a stratum that covers most of the area (SW) and a central stratum (C) for which the southern portion covers the waters between the Magdalen Islands and Cape Breton Island. For each species, an estimate for the sGSL is derived here by adding the estimated abundance in the SW stratum to the estimated abundance in stratum C which was adjusted by the proportion of sightings from that stratum that were made in the sGSL. Kingsley and Reeves (1998) corrected their estimates for sighting biases (e.g., as a function of horizontal distance from the airplane), but not for availability (i.e., the proportion of animals that were at the surface when observations were made) or missed sightings. The authors suggested that the estimate for harbour porpoise could

be biased low by a factor of five due to availability and missed sighting. Here we have applied this correction for harbour porpoise and the roughly comparably sized white-sided dolphin.

Kingsley and Reeves (1998) observed four species of piscivorous cetaceans. Harbour Porpoise (*Phocoena phocoena*) and Atlantic White-Sided Dolphins (*Lagenorhynchus acutus*) were the most abundant cetaceans in the sGSL in the mid-1990s (Table 1). The estimate for the former, but not the latter species, was considered reasonably precise by the authors. Correcting for availability and missed sightings, there were an estimated 18,300 Harbour Porpoise and 23,720 White-Sided Dolphin in the sGSL in the mid-1990s. Though Lawson and Gosselin (2009) reported considerably fewer observations for these species in 2007 (Table 1), it is not possible to determine whether this reflects a decrease in abundance. The other two piscivorous cetacean species observed in the sGSL in the the mid-1990s and 2007 surveys were Minke whale (*Balaenoptera acutorostrata*) and Long-finned pilot whale (*Globicephala melas*). The uncorrected abundance estimates for these species were 220 and 950 individuals, respectively (Table 1).

2.2.1.2 Diet and consumption of Herring

The daily food consumption (*DC*; kg per day) for an individual of each species was estimated using the allometric relationship of Innes et al. (1987); $DC = \alpha\ Mass^{\beta}$, where α and β are estimated to have values of 0.123 and 0.80, respectively. Given that the sGSL is typically seasonally ice-covered during the winter, we assumed that the species spent an average of five months in the area. Note that Read and Brownstein (2003) assumed that seasonal residence of cetaceans in the Gulf of Maine, which does not experience ice cover, was six months.

Harbour Porpoise was the only sGSL cetacean species for which diet information proper to the sGSL was available (Table 1). Fontaine et al. (1994) examined the stomach contents of incidentally caught Harbour Porpoise from May to August 1989 in the western portion of the sGSL. They found that Herring comprised 61% of the diet by weight. The Herring consumed ranged from approximately 25 to 35 cm, with a mode around 30 cm. Diets for the three other species come from other areas (Table 1). It is unlikely that Long-finned pilot whales consume much if any Herring in the sGSL as they are known to mostly be associated with predation on squid, with some consumption of Mackerel (Sergeant 1962). In contrast, Minke whales have been observed feeding on fall spawning Herring in the sGSL (David Cairns, Fisheries and Oceans Canada, pers. comm.).

Among cetaceans,White-Sided Dolphin was estimated to be the largest consumer of Herring, eating over 10,000 tonnes per year (Table 1). Harbour Porpoise was the next largest consumer, followed by Minke whale. Based on the available information, cetaceans were estimated to have consumed around 16,000 tonnes of Herring in 1995 to 1996.

2.2.2 Pinnipeds

Grey Seals (*Halichoerus grypus*) are the main pinniped predators of marine fish in the sGSL (Hammill and Stenson 2000), and this section focuses on them as important consumers of sGSL Herring. Increases in the abundance of Grey Seal occurring in the sGSL have been linked with important increases in the mortality of several demersal fish stocks that are declining in abundance or failing to recover from fishery-induced collapse (Benoît et al. 2011a; Swain and Benoît 2015). Though Grey Seals are predators of pelagic fishes such as Herring (Hammill et al., 2007, 2014a), a link has yet to be made between changes in pelagic fish productivity and Grey Seals in the NW Atlantic.

Though Harbour Seals (*Phoca vitulina*) are present year-round in the sGSL they are much less numerous than Grey Seals (Hammill and Stenson 2000; Robillard et al. 2005) though the

population abundance and trend in the sGSL are poorly known. Harp Seal (*Phoca groenlandica*) and Hooded Seal (*Cystophora cristata*) both come into the Gulf of St. Lawrence to reproduce on the sea ice, but leave the area soon after whelping. Consequently their consumption of fish in the sGSL or on Herring overwintering grounds north of Cape Breton Island (NAFO Div. 4Vn) is considered small to nil (Hammill and Stenson 2000).

2.2.2.1 Grey Seal –Abundance and distribution

The Grey Seal population in the NW Atlantic is composed of three herds: one that breeds in the Gulf of St. Lawrence (mainly in the sGSL), one that breeds on Sable Island, and another that breeds along the Nova Scotia Atlantic coast (coastal Nova Scotia herd). Abundance has grown considerably in the three herds since 1960, most notably for the Sable Island herd for which current abundance is estimated at 400,000 seals (Fig. 5; Hammill et al. 2014b). There was estimated to be around 100,000 Grey Seals in the Gulf herd in 2014.

Grey Seals from the different herds spend time in the sGSL to differing degrees, depending on the season (Benoît et al. 2011b). Since the mid-1990s, the movements of a number of seals from the Gulf and Sable Island herds have been tracked using satellite telemetry (Breed et al. 2006; Harvey et al. 2008; D. Lidgard, Dalhousie University unpublished data). Using these data we estimated the proportion of time that tagged Grey Seals from each herd spent in the sGSL Herring ecosystem, defined as the area covered by NAFO area 4T for May-November and the area for NAFO 4T and 4Vn for December-April. If the movements of tagged seals are representative of the movements of seals in their herd, then these values also represent an estimate of the proportion of seal-days spent in the Herring ecosystem. Grey Seals from both herds were found to be present in higher proportions during the summer and fall, compared to the late winter and early spring (Fig. 6). Seals from the Gulf herd spent the most time in the area, with males spending more time compared to females (e.g., ≥80% vs. 60% in summer). Grey Seals from Sable Island were absent from the area from March to May, and present in small percentages (<10%) in other months.

There were sufficient data to examine whether there were changes over time in the proportion of Sable Island seals that use the sGSL from July to November. Such changes might be expected, for example, as a result of density-dependence. The tracking data were divided into three groups of years and the proportions of time spent in the Herring ecosystem were calculated for each. No long-term trend in usage was apparent across the three time periods: 1995 to 2002 (5.4%), 2003 to 2008 (2.0%), and 2009 to 2014 (5.0%).

Swain et al. (2015a) estimated annual patterns in the finer scale distribution of Grey Seals within the sGSL during the summer for 1971 to 2012. They used the ensemble of satellite telemetry data to estimate movement patterns specific to each of the major grey seal haul-out areas in the sGSL. They then used data from aerial surveys of hauled-out Grey Seals conducted in the mid-1980s, late 1990s and in 2013 to infer changes over the years in the distribution of seals among haul-outs. Combining the haul-out specific movements with the changes in haul-out distribution provided the best available information on long-term changes in summer space use by Grey Seals in the sGSL (details on the method are available in Swain et al. 2015a). During the 1970s, Grey Seals appeared to forage broadly within the sGSL during the summer, with concentrations between the Magdalen Islands and PEI (Fig. 7; left column). Over the decades, their summer distribution appears to have become increasingly concentrated in the Northumberland Strait, west of PEI and south of the Magdalen Islands. During the summer, the distribution of Grey Seals has overlapped considerably with that of Herring (Fig. 7; right column).

2.2.2.2 Grey seal -Diet and consumption of Herring

The diet of Grey Seals in the sGSL has been inferred using prey hard-parts recovered from seal digestive tracts that are typically sampled on or near shore (e.g., Hammill et al. 2007, 2014). These diets reflect feeding that occurred near the sampling site (likely within 30 km) and therefore are unlikely to reflect feeding that occurs further off shore (Benoît et al. 2011c). However, in the case of Herring in the sGSL, their distribution overlaps considerably with that of Grey Seals, both near and further offshore (Fig. 7). It is therefore reasonable to assume that seal consumption of Herring observed near shore might also reflect consumption offshore. From late spring to early fall herring are available to seals in the inshore as well as in offshore areas not covered by diet samples. Whether the contribution of herring to the diet is similar between the inshore and the offshore will depend on the relative abundances of alternate prey and the prey preferences of seals. In the absence of information on prey preferences, we have assumed that the contribution of herring to the diet is similar between the two areas

For late spring to August, Herring comprised 11% of grey seal diets by weight in coastal areas of the sGSL (Hammill et al., 2007). Consumed Atlantic Herring varied in size between 20 and 35 cm, with a mode of 28 cm. The diet of Grey Seals for other times of the year was inferred from samples taken off western Cape Breton and at St. Paul's Island (Hammill et al. 2014), which are likely key areas for migrating and overwintering adult Herring. Those results are available separately for male and female seals, and for prey recovered from stomachs and from intestines. The latter distinction is important because there are correction factors to account for the loss of consumed prey when diet is inferred from intestinal contents, but not for stomach contents. Based on the available information, the diet of male Grey Seals appears to be comprised of around 15.8% Herring in the fall (September-November) and 2.3% in the winter (December-March). In contrast, the diet of female Grey Seals appears to be comprised of around 5.8% Herring in the fall and 25.8% in the winter. Overall, consumed Herring ranged in length from 11 to 35 cm, with a majority in the 26 to 30 cm range.

Prey consumption by Grey Seals was estimated using a bioenergetics model (Benoît et al. 2011a). The daily gross energy intake (GEI; kJ per day) of an individual grey seal was estimated as:

$$GEI_{s,a,m} = \alpha M_{s,a,m}^{\beta} AF\, GP_a\, ME^{-1} \quad (1)$$

where *s*, *a* and *m* index sex, age and month, $\alpha M_{s,a,m}^{\beta}$ is the Kleiber equation (Kleiber 1975) describing the allometric relationship between seal body mass (M) and metabolism, GP is a 'growth premium' that accounts for the additional energy required by rapidly growing young seals, AF is the 'activity factor' that accounts for increased metabolism due to activity in the field, and ME is the 'metabolizable energy' (i.e., assimilation efficiency). Benoît et al. (2011a) estimated sex-specific seal mass at age ($M_{s,a,m}$, in kg) using the Gompertz growth model of Mohn and Bowen (1996), adjusting for seasonal changes due to growth, lactation and reduced feeding during moulting and breeding, following Beck et al. (2003) (Fig. 8). The value of the Kleiber parameters used previously for Grey Seals are $\alpha = 293.75$ and $\beta = 0.75$. The modal value of AF obtained from previous studies is 2.0 (details in Benoît et al. 2011a), while the value for ME based on experiments is 0.83 (Ronald et al. 1984). The estimated values for GP vary as a function of age as follows (Lavigne et al. 1986; Innes et al. 1987):

Age	0	1	2	3	4	5	6+
Growth Premium (GP)	1.8	1.5	1.25	1.1	1.05	1.03	1.0

With this model, consumption is estimated in monthly time steps for each sex and age group (0 to 39 years). Consumption is adjusted for periods of fasting as observed for Grey Seals in the field consisting of 21 days between late December and February for lactating/breeding females

aged 5 years and older, 24 days for adult males (aged 9 years and older) during breeding, and two weeks during the moulting period (May for females, June for males). Annual consumption by a herd is estimated using a 50:50 sex ratio and the age composition and estimated abundance from the population model (Hammill et al. 2014b). Annual consumption in the Herring ecosystem is estimated using the estimated proportion of each herd occurring in the area on a monthly basis (Fig. 6), assuming that 65% of Coastal Nova Scotia herd seals have a seasonal distribution that is like that of Sable Island seals, with the remainder following a distribution like the Gulf herd (M. Hammill, Fisheries and Oceans Canada, pers. comm.).

Estimated consumption of all prey by Grey Seals in the Herring ecosystem has increased from < 10,000 tonnes per year in 1960 to over 120,000 tonnes in 2014 (Fig. 9). The proportion of consumption by Sable Island seals increased from around 2% in 1960 to 17% in 2014. Assuming an average non-Herring prey energy density of 5.3 kJ per g (Trzcinski et al. 2006), a Herring energy density of 7.56, and the diet proportions noted above, Grey Seals were estimated to consume an average of 11,220 tonnes annually during the period from 2005 to 2014.

2.3 FISH

2.3.1 Bluefin Tuna (*Thunnus thynnus*)

2.3.1.1 Abundance and distribution

The most recent assessment of the western Atlantic Bluefin Tuna stock indicates that spawning stock biomass declined almost fivefold during the 1970s, was stable between the mid-1980's to the mid-2000's, and has been increasing since (ICCAT 2014). In contrast to the 11 other indices used in the stock assessment model, the commercial fishery catch per unit effort (CPUE) index for the sGSL has increased rapidly since the early 2000s, recently reaching the highest levels estimated (Fig. 10). Furthermore, the annual proportion of fishing trips that successfully caught one or more Bluefin Tuna in the sGSL has followed a similar trend (Fig. 11). Part of the recent increase in CPUE could be due to changes in catchability resulting from changes in the fishery. Regulatory changes were introduced from 2007 to 2009, such as the adoption of a one-fish-per day per vessel rule in the Prince Edward Island fishery (Hanke and Neilson 2011). Also, the fishery became concentrated in certain months during the 2000s, though there has been a return to pre-2000 fishing patters since the adoption of individual transferable quotas in 2011 (Hanke et al. 2013). However, the fishing gear and method have not experienced any innovations that would alter the catch rates (Hanke et al. 2013). Overall, while the increase in abundance since 2000 may be smaller than what is implied by the CPUE index, it is very likely that local abundance has indeed increased considerably (Vanderlaan et al. 2014). It is not known to what extent the local increase reflects changes in the overall stock versus a shift in distribution into the sGSL, nor is it presently possible to determine what portion of the stock visits the sGSL annually.

Atlantic Bluefin Tuna likely arrive in the sGSL in June to feed and leave later in November. Fishing takes place between late June and into mid to late November (Hanke et al. 2013). Results from satellite telemetry suggest that Tuna occur throughout the central and eastern portions of the sGSL in summer and fall (Walli et al. 2009). The fishery for Bluefin Tuna is concentrated in a slightly more restricted area, in waters north and east of Prince Edward Island (Vanderlaan et al. 2014).

Vanderlaan et al. (2014) found a weak negative relationship between the area of the water column occupied by cold intermediate layer water and the Bluefin Tuna CPUE index for the

sGSL. They hypothesized that this could reflect a direct effect of physiological constraints for Tuna or an indirect effect of prey distribution.

2.3.1.2 Diet and consumption of Herring

There has only been one study of Bluefin Tuna diets for the sGSL. Pleizier et al. (2012) looked at the stomach contents of commercially-caught Bluefin Tuna in Port Hood (sGSL; 35 stomachs) and in nearby Canso (Scotian Shelf; 33 stomachs) in the fall of 2010. Twenty-five of the stomachs from Port Hood came from Tuna caught on or near Fishermen's Bank, an important spawning ground for fall-spawning Atlantic Herring. The stomachs from the Port Hood samples were from large Tuna (approximately 350 kg modal round weight), typical of sizes found in the sGSL. The authors found that Atlantic Herring comprised around 55% and 40% by weight of the diet of Tuna from Port Hood and Canso, respectively. Many of the Herring from the Port Hood samples were gravid, which is consistent with the Tuna feeding on Herring when they are aggregated to spawn. The bulk of the remaining stomach contents comprised unidentified fish (26% and 44% Port Hood and Canso, respectively) and Mackerel (12% and 13%). Though these results provide an indication of Bluefin Tuna diet for the sGSL that is seasonally and spatially limited, and restricted to one year, they nonetheless indicate that predation on Atlantic Herring can be intense at certain times and locations.

Chase (2002) undertook the analysis of the contents of 568 food-bearing stomachs of Bluefin Tuna captured in five fishing areas on the New England continental shelf, over the entire feeding season (June to October) and over five years (1988 to 1992). Across all samples, Atlantic Herring comprised 53% of the stomach contents by weight, followed by Sandlance (23%) and Bluefish (7%). There was considerable variation among areas in terms of the percentage of Herring in the diet, ranging from 3% in areas near Cape Cod and 87% on Jeffrey's Ledge. The consumed Herring varied in length from 18 to 31 cm, with a mean length of around 24.5 cm.

The results above indicate that while there can be considerable spatial and temporal variability in the diet composition, Bluefin Tuna can be an important predator of late juvenile and adult Atlantic Herring. Furthermore, significant spatial association between Herring and Bluefin Tuna in the Gulf of Maine within (Schick and Lutcavage 2009) and across years (Golet et al. 2013) suggest that Herring could be a preferred prey.

Bluefin Tuna have standard metabolic rates that are among the highest of any teleost fish species (Dickson and Graham 2004; Blank et al. 2007), resulting in relatively elevated prey consumption levels. The daily ration (% body mass) for Bluefin Tuna has been estimated using general allometric relationships, bioenergetic modelling, and empirical observations (see Overholtz 2006; Butler et al. 2010). Estimates range from 1% to 4.7%, with an average of approximately 3% which was used here. Tuna caught in the sGSL fishery are generally older (13+ years) and are generally large, with a modal and a mean mass of around 300 kg (Hanke et al. 2013). Assuming a four month residency time in the sGSL, the average individual Bluefin Tuna is estimated to consume a little over one tonne of fish (1,098 kg) in the sGSL per year.

In the absence of absolute estimates of the number of Bluefin Tuna that occupy the sGSL annually during the summer and fall it is difficult to produce a reliable estimate of 4T Herring consumption. However, it is possible to get a rough idea of the magnitude of consumption. Since 2005, harvesters have landed an average of around 580 Tuna per year in the sGSL (Hanke et al. 2013). Assuming that Herring comprise 50% of the diet of Tuna in the sGSL (see above) and taking landings as a minimal annual abundance in the sGSL, a very conservative lower bound of 318 tonnes of 4T Herring consumed is estimated. A perhaps more realistic estimate can be derived using the observed mean catch and the 2005 to 2013 average abundance-weighted 13+ fishing mortality of 0.065 from the western Bluefin Tuna assessment

(calculated from Tables 1 and 2, Appendix 5D, ICCAT 2014). Using the Baranov catch equation and the assumed natural mortality of 0.14 for Tuna (ICCAT 2014), this results in a mid-season average abundance of 9,484 individuals in the sGSL. Assuming a diet comprised of 50% Herring results in an annual consumption of 5,206 tonnes of Herring for recent years. This estimate may still be conservative given that the fishing mortalities in the western Bluefin Tuna assessment are for the entire stock, and the CPUE index for the sGSL suggests a disproportionate abundance increase in the area relative to the entire stock (ICCAT 2014).

2.3.2 Atlantic Cod (*Gadus morhua*)

2.3.2.1 Abundance and distribution

Atlantic Herring are consumed mainly by Cod 35 cm and larger (Hanson 2011), which are generally three years of age or older. Abundance of Cod ages 3+ was low in the early 1970's, increasing rapidly in the late 1970s to a relatively high level of abundance (Fig. 12; from Swain et al. 2015b). The stock collapsed in the late 1980s and early 1990s, and has declined steadily since then. Elevated natural mortality in adult Cod, believed to largely result from predation by Grey Seals, is responsible for the lack of recovery and ongoing stock declines that are occurring despite little fishing (Benoît et al. 2011; Swain and Benoît 2015). Declines have been greatest for the oldest (largest) Cod, such that Cod >75 cm presently represent a much smaller proportion of the population compared to 30 years ago.

Cod overwinter in the Sydney Bight area north of Cape Breton Island, where they overlap spatially with adult Herring. Cod migrate into the sGSL in April, aggregate in the western portion of the sGSL in late spring to spawn, and then disperse in the sGSL to feed. Cod migrate to their overwintering grounds in late fall. During the feeding season, Cod were historically broadly distributed in the sGSL (Swain et al. 2015a). Their distribution expanded as abundance increased in the late 1970s and contracted as it decreased in the early 1990s. Distribution became increasingly concentrated north and northwest of PEI and in the deep water along the slope of the Laurentian Channel and in the Cape Breton Trough over the 1992 to 2012 period.

2.3.2.2 Diet and consumption of Herring

Of all of the predators considered here, diet information is best for Atlantic Cod. There are size-specific estimates of late summer diet for the western portion of the sGSL for a number of years between 1959 and 1980, and for the sGSL as a whole for a number of years since 1987 (Hanson and Chouinard 2002; M. Hanson, Fisheries and Oceans Canada, pers. comm.; Hugues Benoît, Fisheries and Oceans Canada, unpubl. data). Furthermore there are data for areas where sGSL Cod are aggregated during other times of the year for many years since 1990s (Schwalme and Chouinard 1999; M. Hanson, Fisheries and Oceans Canada, pers. comm.; Hugues Benoît, Fisheries and Oceans Canada, unpubl. data).

The diet of Cod is size-specific and Cod < 30 cm consume very little Herring (Hanson 2011; Hugues Benoît, Fisheries and Oceans Canada, unpubl. data). The length of Herring consumed generally increases with the length of their Cod predator, though Cod larger than about 45 cm can consume the full size range of Herring (Fig. 13). The available data were used to estimate the consumption of Herring by Cod in four size groups (in cm); 15 to 29, 30 to 44, 45 to 59 and ≥ 60 cm. For data that were collected during standardized surveys (annual September research vessel (RV) surveys and an April 2011 survey of the southeastern Gulf of St. Lawrence), results for individual Cod within a size group were first averaged within fishing sets and then weighted by the relative abundance of Cod in the size group in the set catch to calculate an overall average diet. Because the sampling of sets was incomplete, weighting by the survey design was not used.

In the first analysis, the data from years in which there was sGSL-wide sampling during RV surveys were used to estimate average annual diets for the sGSL as a whole and for the western portion of the area only, defined as the area west of 63° longitude. The aim was to determine whether the restricted sampling that occurred in most years prior to the mid-1980s (Hanson and Chouinard 2002) could nonetheless produce estimates of the proportion of Herring in the diet of Cod that reflect patterns for the whole area. A close correspondence between whole and restricted-area estimates of the proportion of Herring in the diet was found for all size classes of Cod, confirming that the average estimates from all years of sampling could indeed be used (Fig. 14).

Herring occurred in small proportions of the diet of Cod during the early 1970s, were essentially absent from the diets around 1980 and have been at more elevated though annually variable levels since the mid 1980s (Fig. 15a). During this latter period, Herring were generally < 20% (by weight) of the diet of Cod 30 to 44 cm, around 25% of the diet of 45 of 59 cm Cod, and around 50% (and occasionally upwards of 90%) of the diet of Cod 60 cm and above. The observed short-term variability in diet composition likely reflects sampling variability and perhaps some changes in Cod diet as a result of changes in the abundance of Herring and other prey.

To examine the relationship between diet composition and the relative abundance of Herring, we used the standardized biomass index (mean kg per tow) for Herring ≥ 20 cm from the September research vessel trawl survey. This index reflects the joint abundance of spring and fall spawning Herring and is free of any modelling assumptions used in the assessment of Herring. Though there is some interannual variability in this index as a result of the schooling nature of Herring, the patterns in this index match those from the assessment of the stock. Specifically, both show a low abundance during the 1970s and into the early 1980s, a rapid recovery of the stock during the 1980s to a peak in the late 1980s, a slight decline in the mid to late 1990s, followed by a recovery and then a more recent decline (Fig. 15a; LeBlanc et al. 2015). To smooth over the high frequency interannual variability in the abundance index, we fit a general additive model (GAM) with eight degrees of freedom for the smooth term to the log-transformed index (Fig 15a, black line). The proportion of Herring in the diet of Cod in size group s and year i, $P_{s,i}$, was modelled as a function of the smoothed Herring abundance index in year i,h_i, using the following functional response model:

$$P_{s,i} = \frac{\gamma_s}{1+\tau \cdot \exp(-\varphi \cdot (h_i - \omega))} \qquad (2)$$

where γ_s is a Cod size-group specific asymptotic proportion of Herring in the diet, τ is a shape parameter and φ and ω control the location of the inflection point for the curve. Note that only γ_s was considered to vary among size groups. This model provided a reasonable fit to the observed diet proportions, with a rapid increase in the proportion of Herring in the diets as the smoothed abundance index increased from around 8 to 16 kg per tow (Fig. 15b). This relationship produces a rapid increase in the proportion of Herring in the diet of Cod of various sizes during the 1980s that is consistent with the dramatic increase that occurred between the 1980 and 1987 Cod diet samples (Fig. 15c).

Diet information outside of September is considerably more limited. Based on the preceding analysis, we assumed that diet proportions in those months during the period from 1990 to present varied around month-specific average asymptotic levels. Aggregating data by month and size group, and taking into consideration available sample sizes, it appears that the proportion of Herring in the diet is roughly constant during the first nine months of the year (Fig. 16). The proportion then peaks in October and November, before returning to a lower level in December (Table 2). Based on averages over the respective periods, month-specific values of γ_s for the consumption estimation were used (Table 2a).

To estimate the consumption of Herring by Cod, we used the bioenergetics approach of Overholtz and Link (2007) and Tyrrell et al. (2008), among others. Specifically, monthly size-specific consumption by Cod was estimated based on average stomach content weights and gastric evacuation rates (Eggers 1977; Elliott and Persson 1978; Pennington, 1985):

$$C_{m,l} = (30.42 * 24) * S_{m,l} * R_m \quad (3)$$

where $C_{m,l}$ is the monthly consumption of prey (in g) by an individual Cod of length l (cm), 30.42 is the average number of days in a month, 24 is the number of hours in a day, $S_{m,l}$ is the mean stomach content mass (g) by month and length, and R_m is the evacuation rate per hour, which varies as a function of temperature T_m. R_m was modelled here using monthly temperature averages:

$$R_m = \alpha\, e^{\beta \cdot Tm} \quad (4)$$

where $\alpha = 0.004$ and $\beta = 0.115$ are constants (Durbin et al. 1983; Overholtz et al. 2000). Mean temperatures occupied by Cod ≥ 30 cm were estimated using survey observations of Cod abundance and bottom-temperature using the approach of Perry and Smith (1994). Annual values were estimated from the data collected during the September research vessel survey, and were assumed to represent conditions experienced by Cod from July to October (Fig. 17). Observations from surveys conducted during other times of the year were used to estimate average values for winter (December to March; 4.9°C), spring (April to June; 2.1°C) and November (2.2°C) (see Benoît 2013 for details on those surveys). As a result of limited information, and the fact that there is little interannual variation in temperature in the deep waters where Cod overwinter (Benoît et al. 2012), those values were assumed to be fixed across years.

The length and month specific mean stomach content masses $S_{m,l}$ were estimated using data from two sources. The first is data from seasonal Cod condition sampling which has been undertaken each year since 1991. Part of that sampling involved weighing the stomachs (lining and content) of individual Cod. These values were converted to estimates of stomach content mass by subtracting the mass of the stomach lining estimated using the following empirical relationship with fork length (in mm) (Denis Chabot, Fisheries and Oceans Canada, unpubl. data):

$$\log_{10}(\text{lining mass}) = -7.118 + 3.084 \cdot \log_{10}(\text{length}) \quad (5)$$

The resulting estimates include the mass of mucus and all other stomach contents. The second source of data is the stomach content observations used to derive the diets. The sum of prey weights, excluding the weight of mucus, rocks, foreign material and parasites, was taken as the stomach content weights. In order to derive estimates of $S_{m,l}$ we fit a linear model of the following form to the data from the two sources:

$$\log_e(\text{content mass}) \sim \text{Source} + \text{Month} + \text{Length} + \text{Month*Length} \quad (6)$$

where source is either Cod-condition sampling or observed prey weights, in both cases including empty stomachs. A small constant was added to content mass to ensure a value greater than zero (log defined).

This model provided a reasonable fit to the observations, explaining around 45% of the variation in content mass (Fig. 18; Table 3). Predicted masses were greater for the Cod-condition sampling observations, which makes sense because these include the weight of non-prey items (e.g., mucus, rocks, parasites). Predicted weights were considerably lower during winter months, a period of limited feeding for Cod (Schwalme and Chouinard 2009), and were greatest during the summer feeding period. Predictions from equation 6 for prey masses (i.e., source = diet data) were used to estimate consumption in equation 3.

Annual consumption of Herring by sGSL Cod was estimated using $C_{m,l}$, the annual proportion of Cod at length *l* as a function of age *a* from sampling during the annual survey, $p_{l\text{-}a,y}$, and estimates of demographic parameters from the Cod assessment model incuding beginning of year numbers at age ($N_{a,y}$), annual age-dependent fishing mortalities ($F_{a,y}$), and annual age-group dependent natural mortalities ($M_{a,y}$) (Swain et al. 2015b):

$$C(h)_y = \sum_{m=1}^{12} \sum_{a=2}^{12+} \sum_l C_{m,l} \cdot d_{m,l,y} \cdot p_{l-a,y} \cdot N_{a,y} \exp\left((-F_{a,y} - M_{a,y}) \cdot m/12\right) \quad (7)$$

where $C(h)_y$ is the total consumption of Herring by sGSL Cod in year *y* and $d_{m,l,y}$ is the proportion of Herring in the diet of Cod of length *l* in month *m* and year *y*, derived using equation 2 and the assumed seasonal values of γ_s. Within season growth of Cod is not included in the model for simplicity, and instead late summer lengths at age were assumed.

As a result of low Cod abundance during the early 1970's and negligible amounts of Herring in Cod diets up to the early 1980s, estimated consumption of Herring was very low until the mid 1980s (Fig. 19). With increases in Herring abundance and the inferred increased prevalence in the Cod diets, estimated consumption increased dramatically after 1985 to around 80,000 tonnes per year. Estimated consumption then decreased equally rapidly as the Cod stock collapsed, varying around 10,000 tonnes per year for much of the 1990s before continuing to decline with declining Cod abundance since 2000.

2.3.3 White Hake (*Urophycis tenuis*)

2.3.3.1 Abundance and distribution

The abundance of two year old juvenile White Hake in the southern Gulf of St. Lawrence has varied with little long term trend since the late 1970s (Fig. 20; Swain et al. 2015c). In contrast, the abundance of adult White Hake declined considerably in the late 1980s and early 1990s, and has varied at a relatively low level through much of the 2000s. A combination of fishing mortality and rising natural mortality on adults caused the large decline, while further increases in natural mortality to high levels has prevented population recovery despite a moratorium on directed fishing in place since 1995 (Swain and Benoît 2015).

During the summer feeding season, White Hake have a bimodal distribution with respect to depth in the sGSL, occurring in shallow inshore areas and in deeper water along the slope of the Laurentian Channel and in the Cape Breton Trough. Since the 1970s, White Hake were progressively lost from the shallow inshore areas, becoming increasingly concentrated in the deep water areas of the southern Gulf (Fig. 21). By the late 2000s, less than 5% of the population occurred in inshore areas, compared to generally > 60% in the 1970s. The shift in distribution appears to largely be related to an enhanced risk of predation by Grey Seals in the nearshore areas formerly and currently occupied by White Hake (Swain et al. 2015a).

2.3.3.2 Diet and consumption of Herring

Diet information for White Hake in the summer and early autumn was available based on sampling of inshore Hake in and around St. Georges Bay, NS in the early 2000s (Hanson 2011) and both inshore and offshore Hake during the annual multispecies trawl surveys of 2004 to 2006 (H. Benoît, Fisheries and Oceans Canada, unpubl. data). No Herring were found in the diet of White Hake in offshore areas (n = 237; H. Benoît, Fisheries and Oceans Canada, unpubl. data), which is consistent with the general absence of Herring from those areas at that time of the year. In nearshore areas, there were strong ontogenetic patterns in the proportion of Herring in the diet. Hanson (2011) found no Herring in the diet of 25 to 34.9 cm White Hake while Benoît (Fisheries and Oceans Canada, unpubl. data) found that Herring comprised 32% of their diet over a spatially broader sampling area. The amount of Herring in the diet rose very rapidly to 89% for Hake between 45 and 49.9 cm, dropping with further increases in Hake size as

Mackerel comprised an increasing proportion of the diet (Hanson 2011). These diet data for White Hake in inshore waters were assumed to reflect patterns for the feeding season, when both Hake and Herring are present. In the absence of data for other seasons, we assumed that the size-specific diet of White Hake was like that of Cod given coarse similarities in their distribution with respect to that of Herring in those seasons. Furthermore, given the absence of White Hake diet information prior to the 2000s, we assumed that the proportion of Herring in the diet varied as a function of Herring abundance following equation 2, but with size-specific asymptotic proportions (γ_s) (Table 2b).

Consumption of Herring by White Hake was estimated using the same bioenergetics model as for Cod (equations 3 and 4). White hake and Cod have remarkably similar diel cycles in weight-at-length (Fig. 12 in Swain et al. 2011) indicative of similar patterns in feeding activity. Furthermore, the two species also have very similar annual patterns in weight-at-length (Fig. 16 in Swain et al. 2011), indicative of similar seasonal bioenergetics dynamics. Consequently, the $S_{m,l}$ functions derived for Cod (Fig. 18) were used for White Hake. Values for the evacuation rate, R_m, were derived using the mean temperatures occupied by White Hake ≥ 25 cm using data from the same surveys as were used for Cod. Occupied temperatures for the June-October period excluded the offshore strata that are also occupied by the deep water White Hake that do not feed on Herring in those months (strata 415,425, 437, 438, 439) (Fig. 17).

Annual consumption of Herring by sGSL White Hake was estimated using equation 7, incorporating the annual proportion of hake at length *l* as a function of age *a* from sampling during the annual survey and estimates of demographic parameters from a recent population model developed for a sGSL White Hake recovery potential assessment (Swain et al. 2015c). However, there were two differences compared to the model used for Cod. First, the model for White Hake treated ages 2 to 10+ for 1978 to 2013, instead of ages 2 to 12+ for 1950 to 2014 for Cod, consistent with the most recent modelling. Second, the abundance of White Hake ($N_{a,y}$) during June to October was adjusted to include only those fish that occur in nearshore areas, by multiplying $N_{a,y}$ by the estimated proportion of the population occurring in those areas based on observations from the survey (Fig. 21).

Annual consumption of Herring by White Hake was modelled to have increased to a peak level of over 12,000 tonnes in the mid-1980s, declining considerably after 1990 (Fig. 22). Annual consumption declined more slowly after 1995, and is estimated to be below 500 tonnes since 2010.

2.3.4 Other demersal fish

Four other species of sGSL groundfish were found to consume late juvenile and adult Herring in diet sampling undertaken during the September surveys from 2004 to 2006: Greenland Cod (*Gadus ogac*), Longhorn Sculpin (*Myoxocephalus octodecemspinosus*), Shorthorn Sculpin (*M. scorpius*) and Wrymouth (*Cryptacanthodes maculatus*). In all cases, Herring were consumed by larger fish (> 20 cm), and represented a quarter or more of the estimated diets for some species and sizes (Table 4). However, consumption of Herring by these species was not estimated because these species are much less numerically abundant than Cod in the annual trawl survey (Fig. 23). Though their catchability to the survey may differ from that of Cod, it is highly likely that their consumption of Herring is much smaller than that of Cod and other predators and excluding them is unlikely to significantly bias the global estimates of consumption.

3. TOTAL CONSUMPTION OF NAFO 4T HERRING BY PREDATORS

Based on the preceding section, it is clear that the predators considered here are all important consumers of late juvenile and adult sGSL Herring. Estimating their joint annual consumption

required additional assumptions to those made above. Because too many assumptions concerning abundance are required to estimate the consumption by cetaceans, especially for years other than 1995 and 1996, this group has been excluded from the following calculations.

The first assumptions that were required relate to possible changes in diet as a function of Herring abundance for predators other than Cod. As these are all generalist predators, it seems reasonable to make similar assumptions as were made for Cod. We therefore used the model in equation 2 to model changes in diet, assuming that the recent diet value indicated in the text for each species represent asymptotic diet values. As noted above, there is evidence from diet samples of cormorants made on the Magdalen Islands in the late 1970s that the amount of Herring in the diet could be elevated despite low Herring abundance, though it is not clear whether this was a localized phenomenon or whether it was true for cormorants throughout the Gulf. To examine the sensitivity of consumption estimates to the assumption of diet changes as a function of Herring abundance, we also calculated consumption assuming no diet change for all species except Cod, where there are data to support the assumption.

The second set of assumptions concerned Bluefin Tuna, and specifically how abundance in the sGSL related to the CPUE index and how it varied in years prior to the index. The more realistic estimate of average total consumption for 2005 to 2013 (section *2.3.1.2*, 10,400 t of prey per year) was divided by the average CPUE value for the same period to obtain a consumption ratio. This ratio was then multiplied by the CPUE values to obtain annual total consumption values. These were in turn multiplied by the estimated proportion of Herring in the diet, using equation 2 and assuming an asymptotic diet composition of Herring of 50%. Furthermore, because the current population assessment models for sGSL Herring begin in 1978, consumption estimates were required for that same period. We therefore assumed that the value of the CPUE index for 1978 to 1980 was equal to the mean for the three years that followed (1981 to 1983) and the value for 2014 was equal to the mean for the three years that preceded it (2011 to 2013).

Consumption of Herring was low in the early 1970s, because of low abundance of all predators other than White Hake, and low Herring abundance (Fig. 24). In the model that assumed temporally variable diets, consumption declined to a very low level by the late 1970s as a result of low Herring abundance. With recovery of both the sGSL Cod and Herring stocks, estimated annual consumption peaked rapidly at over 100,000 tonnes in the mid-1980s and then declined almost as quickly as the Cod stock collapsed. Declines in estimated consumption by groundfish since 1990 have been offset by increases in estimated consumption by Grey Seals and Northern Gannets, and more recently by increased predation by Tuna. Though consumption by cormorants has increased considerably since 1970, their contribution to overall predation on sGSL Herring appears to be small. Estimated consumption of Herring by fish, avian and Grey Seal predators in 2013 was 34,800 t, an amount that is comparable to the landings in that year of around 36,000 t (LeBlanc et al., 2015).

Assuming temporally invariable diet composition for all predators except Cod by design affects almost exclusively the consumption estimates prior to the mid-1980s when Herring abundance was low (Fig. 24b). Estimated consumption was around 50% greater in the early 1970s and more than ten-fold greater for the late 1970s and early 1980s when diet was assumed fixed. However, this assumption is unlikely to be accurate for most or all of these predators given the very low abundance of Herring in those years and the generalist nature of the predators. These consumption estimates therefore likely represent a biased upper bound, all else being equal.

Estimated consumption of Atlantic Herring by fish, avian and seal predators in 1995 and 1996 in both scenarios was around 26,800 t. The estimate of predation by cetaceans for those same years of 15,800 t indicates that this group of predators can be a relatively important contributor

to sGSL Herring mortality. Absence of information to estimate consumption for other years means that the overall magnitude and trend in total estimated consumption may differ substantially from what is shown in Fig. 24.

4. DISCUSSION

A number of important uncertainties still remain with respect to predation mortality on sGSL Herring despite the efforts presented above. Key among them are consumption by cetaceans, the accuracy of estimates for Bluefin Tuna and the extent to which diets of predators have changed over time. Together, these uncertainties are likely to have led to a large underestimation of predation on Herring in most, if not all, years. Changes over time in consumption by cetaceans, and to a lesser extent changes in predator diets, also mean that the trends in consumption estimated here are likely to be inaccurate. Although little can be done to correct this retrospectively, ongoing monitoring of predator abundances and diets will likely improve our understanding in the future. For example, another Trans North Atlantic Sightings Survey (TNASS) for cetaceans is planned for 2016. The results from that survey and the 2007 TNASS survey, once corrected for availability and perception biases, combined with the 1995 and 1996 survey (Kingsley and Reeves 1998), will provide a reasonable basis for estimating coarse trends in cetacean abundance in the sGSL since the mid-1990s. Likewise ongoing work aimed at developing fishery-independent indices of Bluefin Tuna abundance using hydroacoustics and studies aimed at better characterizing the diet of this predator in the sGSL will improve estimation of Herring consumption.

Error propagation methods based on Monte Carlo simulations can readily be used to estimate the uncertainty surrounding consumption estimates in light of the uncertainty in input data and parameters (Overholtz and Link 2007). To the extent that the models and inputs used are accurate and the uncertainty in inputs is well characterized, the resulting overall uncertainties will be correct. However, if for example the models used are incorrect or if there are biases in the inputs that are not adjusted for, true consumption can be quite different than what is implied by the estimates and associated uncertainty. Given the important issues noted above we felt that it was not possible to correctly estimate overall consumption, let alone its uncertainty, for sGSL Herring. Providing uncertainty bounds for the estimates presented here risked giving a false sense of confidence in the consumption time series overall. Instead we believe that our results are most appropriate for gauging the general potential magnitude of predation on sGSL Herring and for considering possible changes over time in the relative importance of certain predators. For example, like in other ecosystems, it is clear that predation mortality on Herring can be of comparable or greater magnitude than fishing mortality. Futhermore, it is very likely that decreased predation by gadoid groundfish since 1990 has been offset to some degree by increased predation by Grey Seals and gannets in the sGSL. With continued growth of the Northwest Atlantic Grey Seal population and of the number of Bluefin Tuna that feed in the sGSL in summer, combined with possible recovery of cetacean populations (Magera et al. 2013), it is quite possible that predation on sGSL Herring will increase in the short to medium term.

The focus of this report has been on consumption of Herring by major predators, with the aim of better understanding the impact of predation on the spring and fall spawning stocks. Clearly some reciprocal effect of Herring on its predators is to be expected. As noted previously, within year and interannual distribution of Bluefin Tuna in the Gulf of Maine is associated with Herring distribution suggesting that Herring may have some bottom-up effect on their predator. Similarly, interannual trends in return rates of repeat spawning Atlantic salmon that likely recondition in the sGSL has been associated with the availability of forage fish including Herring (Chaput and

Benoît 2012), again consistent with a bottom-up effect on predators. The productivity of these predator species may therefore depend on how sGSL Atlantic Herring are managed.

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TABLES

Table 1. Estimated abundance, mean body mass, and the incidence in the diet and consumption of Herring for the four piscivorous cetacean species surveyed by Kingley and Reeves (1998) in 1995.

Species	Mean mass (kg) [1]	Survey 1995 (Kingsley and Reeves 1998) Area: SW stratum + portion C stratum	Survey 2007 (Lawson and Gosselin 2009) Area: Strata G/EW	Proportion Herring in diet	Consumption (tonnes)
Harbour Porpoise (*Phocoena phocoena*)	45	Count =61 Estimate=3,656 CV~50% Corrected estimate = 18,300	Count = 21	0.61 [2]	4,390
White-Sided Dolphin (*Lagenorhynchus acutus*)	120	Count=112 Estimate=4,744 CV~50% Corrected estimate = 23,720	Count = 39	0.50 [3]	10,220
Minke whale (*Balaenoptera acutorostrata*)	4,500	Count=7 Estimate=220 CV~65%	Count = 8	0.34 [3]	1,170
Long-finned pilot whale (*Globicephala melas*)	1,800 (males 2,300, females 1,300)	Count=92 Estimate=950 CV~80%	Count = 15	Very minor [4]	na
All					15,780

For the 1995 survey, the table provides a summary of the number of individuals observed, the estimated abundance correcting only for sighting bias, an approximate coefficient of variation (CV) for that estimate based on the CVs in the two selected strata, and for two species, an estimate of abundance that is roughly corrected for availability bias and missed sightings. For the 2007 survey (Lawson and Gosselin 2009), only observed counts are presented. The reference for mean mass of cetaceans (superscript 1) is Kenney et al. (1987). References for the proportion Herring in the diet are in superscript (2 = Fontaine et al. 1994; 3 = Read and Brownstein 2003; 4 = Sergeant 1962).

Table 2a. Size-group specific asymptotic proportion of Herring in the diet of Atlantic cod by monthly periods.

Size-group (cm)	Jan. - Sept.	Oct. – Nov.	Dec.
< 30	0	0	0
30-44	0.031	0.195	0.031
45-59	0.248	0.487	0.248
60+	0.490	0.609	0.490

Table 2b. Size-group specific asymptotic proportion of Herring in the diet of White Hake by monthly periods.

Size-group (cm)	Jan. – May (all)	June – Oct. (inshore only)[1]	Nov.-Dec. (all)
< 25	0	0	0
25-34.9	0.031	0.320	0.031
35-39.9	0.031	0.742	0.031
40-44.9	0.031	0.775	0.031
45-49.9	0.248	0.890	0.248
50-54.9	0.248	0.836	0.248
55-59.9	0.248	0.709	0.248
60+	0.490	0.704	0.490

[1] These diet proportions are relevant only for White Hake in inshore waters. The value for the 25 to 34.9 cm group is from Benoît (Fisheries and Oceans Canada, unpubl. data) and values for the other groups are from Hanson (2011). There are no Herring in the diet of White Hake in offshore waters during June to October.

*Table 3. Results of the analysis of Atlantic Cod stomach mass data using a linear model of the form $\log_e$(content mass) ~ Source + Month + Length + Month*Length. Note that data from months 1-3 (January-March) were aggregated prior to fitting the model.*

Parameter	Estimate	S.E.	t value	P-value
Intercept	-1.8641	0.1588	-11.74	< 2e-16
Source	-0.8027	0.0136	-59.05	< 2e-16
month4	0.6657	0.1799	3.70	0.00022
month5	1.1679	0.1838	6.35	<0.00001
month6	1.7427	0.1850	9.42	< 2e-16
month7	1.2627	0.1723	7.33	<0.00001
month8	0.3427	0.1749	1.96	0.05009
month9	0.0400	0.1620	0.25	0.80523
month10	0.4763	0.1771	2.69	0.00715
month11	-0.1942	0.2081	-0.93	0.35060
month12	0.1048	0.3639	0.29	0.77327
length	0.0613	0.0036	17.15	< 2e-16
month4:length	0.0181	0.0042	4.35	0.00001
month5:length	0.0176	0.0041	4.24	0.00002
month6:length	0.0026	0.0041	0.65	0.51900
month7:length	0.0132	0.0039	3.43	0.00060
month8:length	0.0213	0.0039	5.42	<0.00001
month9:length	0.0283	0.0037	7.75	<0.00001
month10:length	0.0170	0.0040	4.23	0.00002
month11:length	0.0195	0.0047	4.15	0.00003
month12:length	0.0189	0.0086	2.19	0.02876

Table 4. Estimated proportion of Herring in the diet of four sGSL demersal fishes (by size group), based on diet sampling undertaken during the 2004, 2005 and 2006 September research vessel bottom trawl surveys of the sGSL.

Predator	Length class (cm)	N	Proportion Herring in the diet
Greenland Cod	≤30	36	0
	>30	68	0.27
Longhorn sculpin	≤20	139	0
	>20	311	0.04
Shorthorn sculpin	≤20	39	0
	21-30	94	0.22
	>30	58	0.28
Wrymouth	41-88	19	0.49

FIGURES

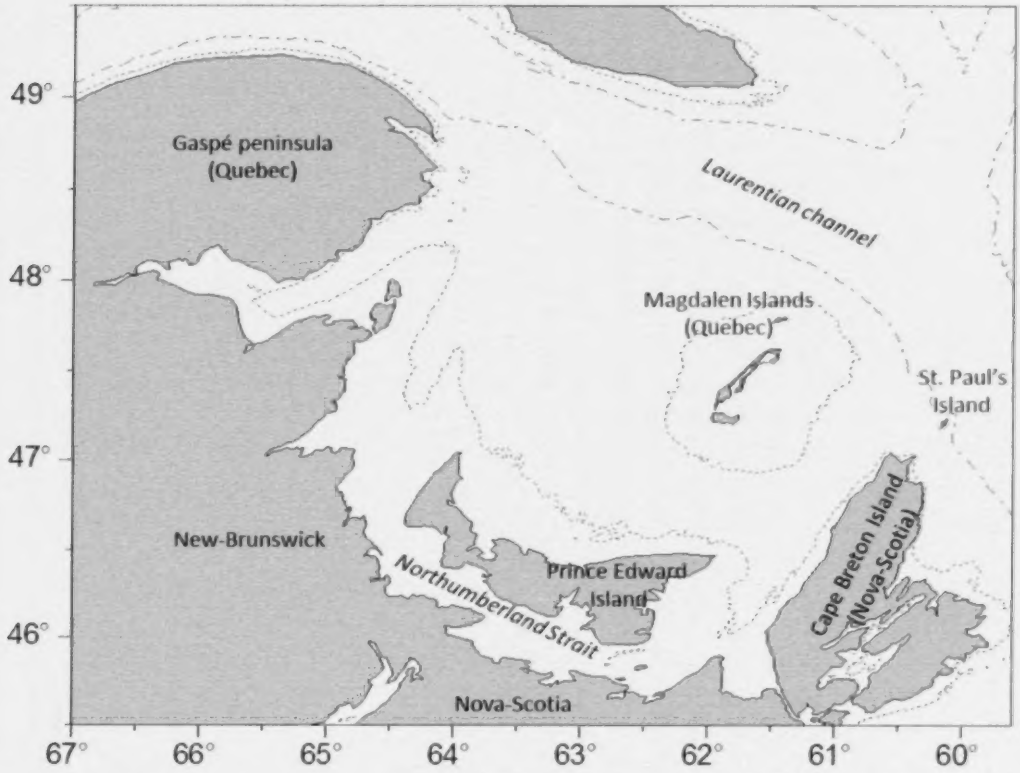

Figure 1. Map of the area occupied by southern Gulf of St. Lawrence Atlantic Herring with place names noted in the text. The grey dotted and dashed lines indicate the 50 m and 250 m depth contours respectively.

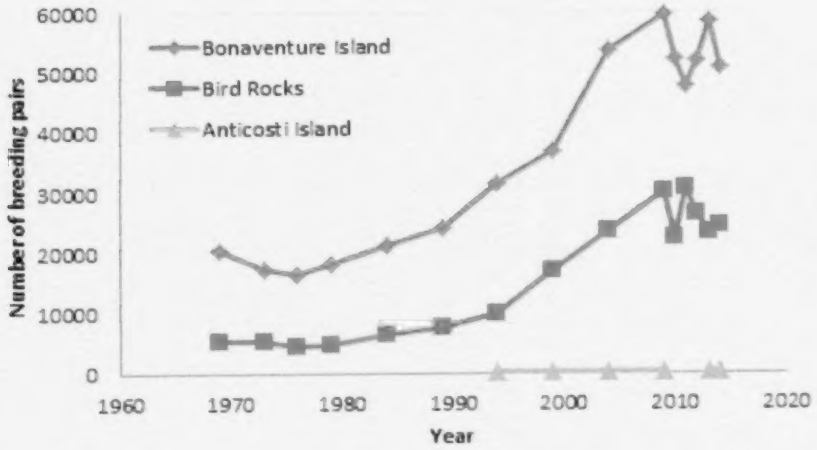

Figure 2. Trends in the number of breeding pairs of Northern Gannets at the three colonies of the Gulf of St. Lawrence (from Rail et al. 2013; J.-F. Rail unpublished information).

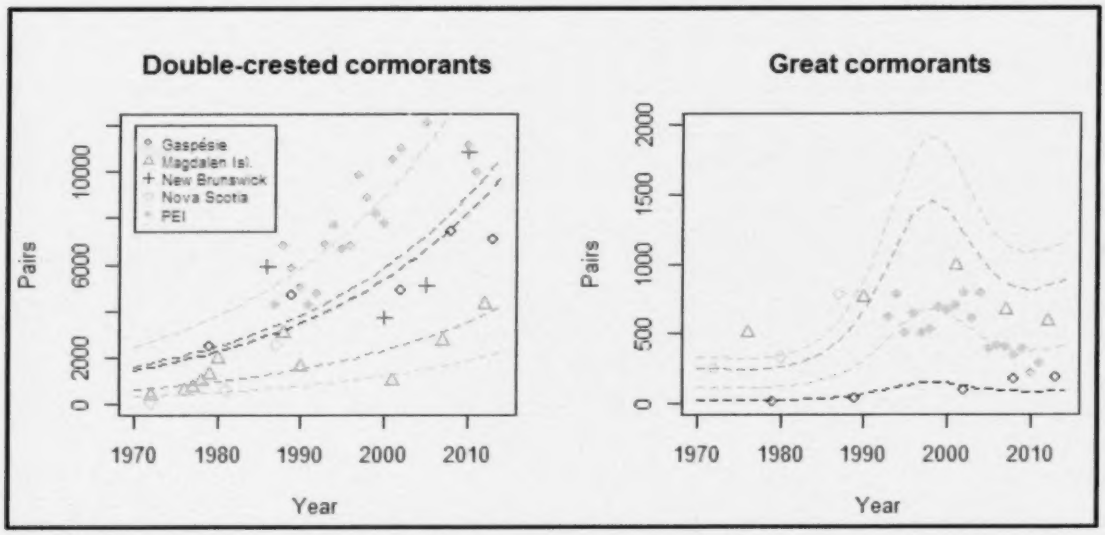

Figure 3. Survey estimates of cormorant breeding pair numbers at colonies bordering the southern Gulf of St. Lawrence, grouped by province or region (points), for double-crested cormorants (left panel) and great cormorants (right panel). The lines are model estimates of abundance trends for each province/region.

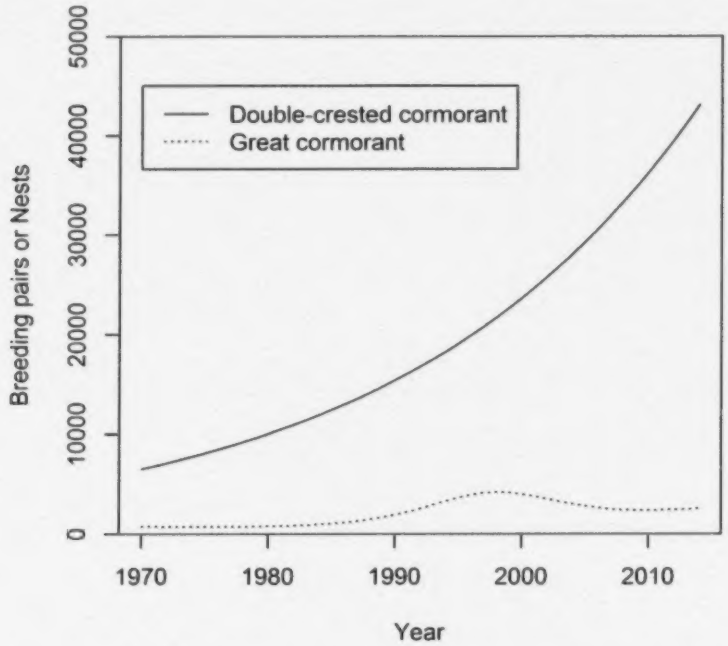

Figure 4. Total estimated number of breeding pairs (active nests) of Double-crested (P. auritus) and Great (P. carbo) cormorants in colonies bordering the sGSL. Counts were estimated using linear or additive models fit to intra- and inter-area counts (details in the text).

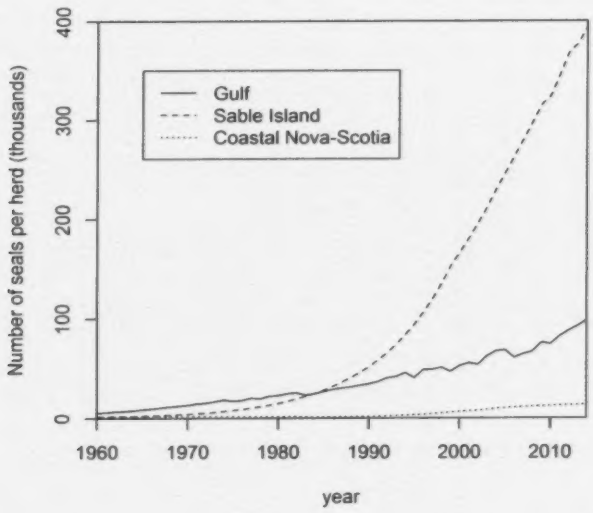

Figure 5. Trends in the abundance of grey seals in the three herds of the NW Atlantic population (from Hammill et al. 2014b).

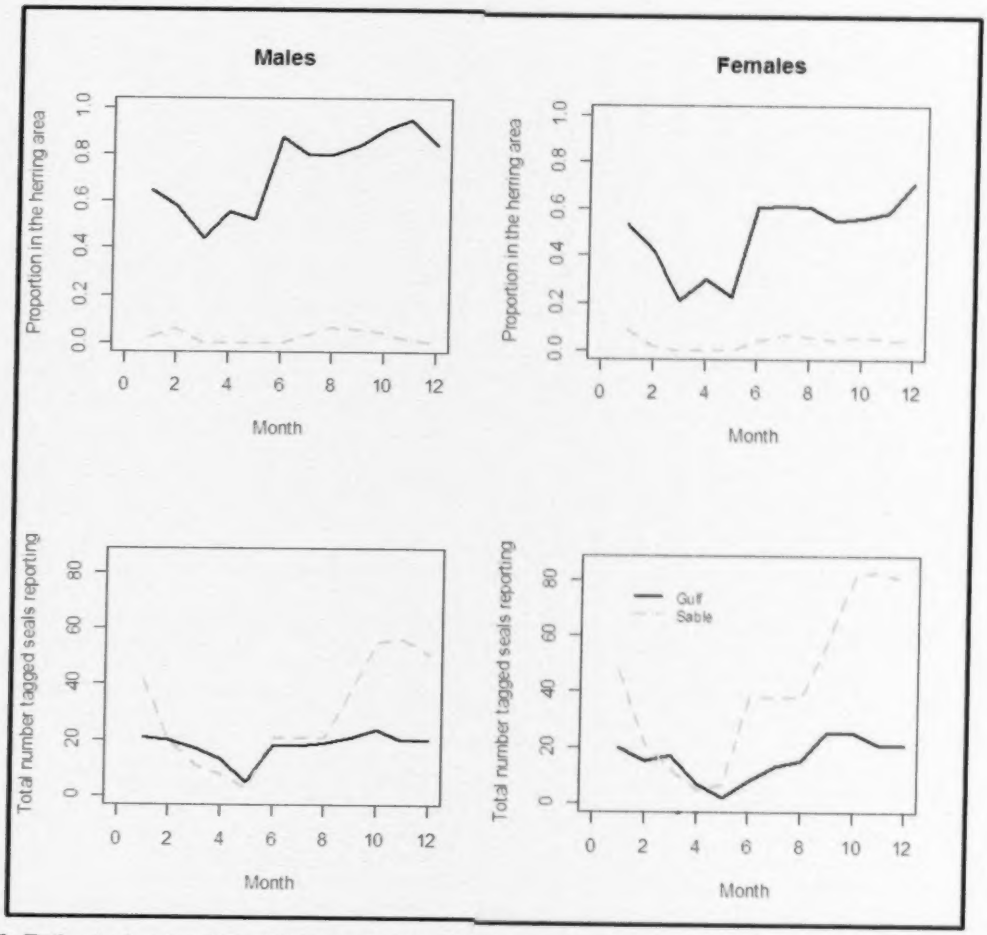

Figure 6. Estimated proportion of time spent by satellite-tracked Grey Seals in the sGSL Herring ecosystem (top row) and total number of tagged seals in the NW Atlantic (bottom row) as a function of month (x-axes), herd (line type) and sex (columns; right-males, left-females). The lower panels show data availability and therefore provide an indication of the confidence that might be placed on the estimates of space use shown in the upper panels.

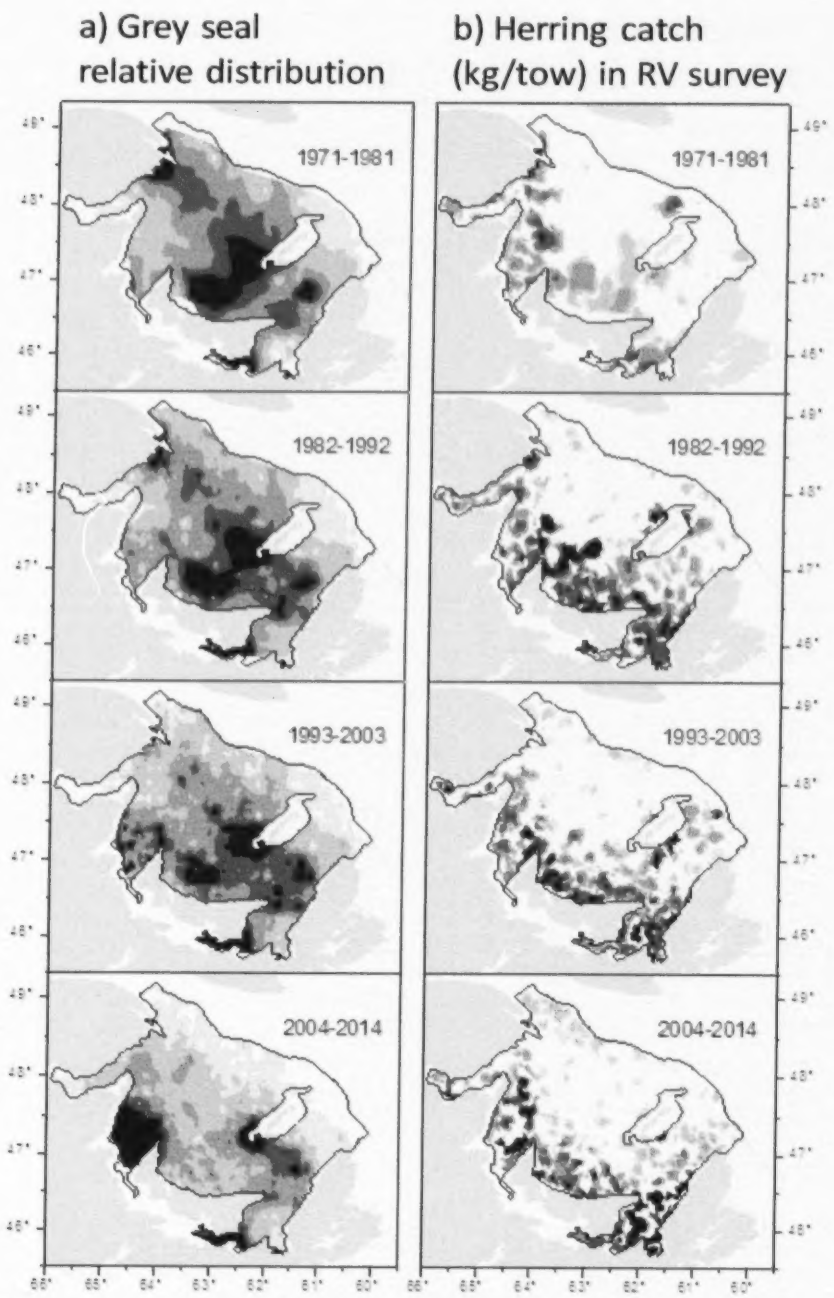

Figure 7. Estimated relative summer distribution of Grey Seals (a; left column) and Herring (b; right column) in four eleven-year blocks (rows). The lightest grey shade represents the 5th percentile of density and the black areas represent the 95th percentile. The distribution of Grey Seals was estimated using the method of Swain et al. (2015) whereas the distribution of Herring is based on standardized catches from the annual bottom-trawl survey of the sGSL. Note that in both columns, the distribution is presented for the survey area only (outlined using a black line).

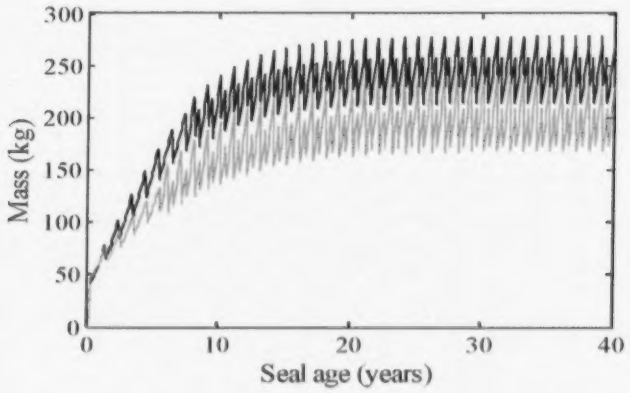

Figure 8. Individual mass (kg) of male (black line) and female (grey) Grey Seals as a function of age, including seasonal changes (from Benoît et al. 2011a).

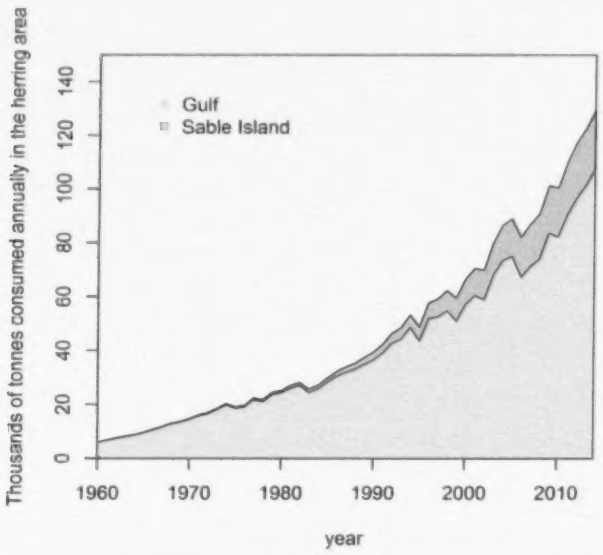

Figure 9. Trends in the estimated consumption of all prey species by Grey Seals in the Herring ecosystem. Estimates are presented for the Gulf herd and the Sable Island herd, with consumption by Coastal Nova-Scotia seals grouped into each (65% into Sable, 35% into Gulf, see text for details).

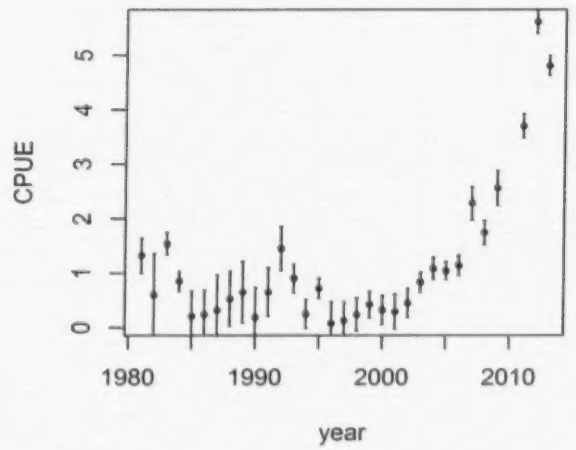

Figure 10. Catch per unit effort (CPUE; ±2 standard errors) for Atlantic Bluefin Tuna in the Gulf of St. Lawrence (ICCAT 2014).

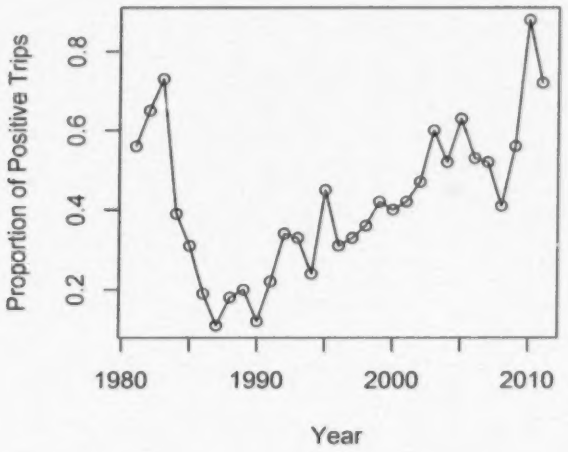

Figure 11. The annual proportion of fishing trips that successfully caught one or more Bluefin Tuna in the southern Gulf of St. Lawrence (Hanke et al. 2013).

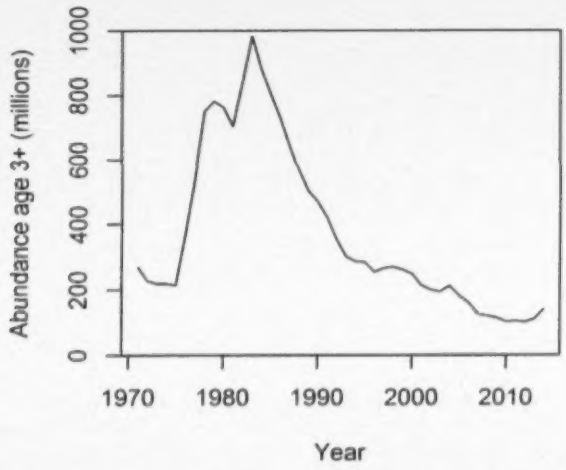

Figure 12. Abundance of sGSL Cod based on statistical catch-at-age modelling (Swain et al. 2015b).

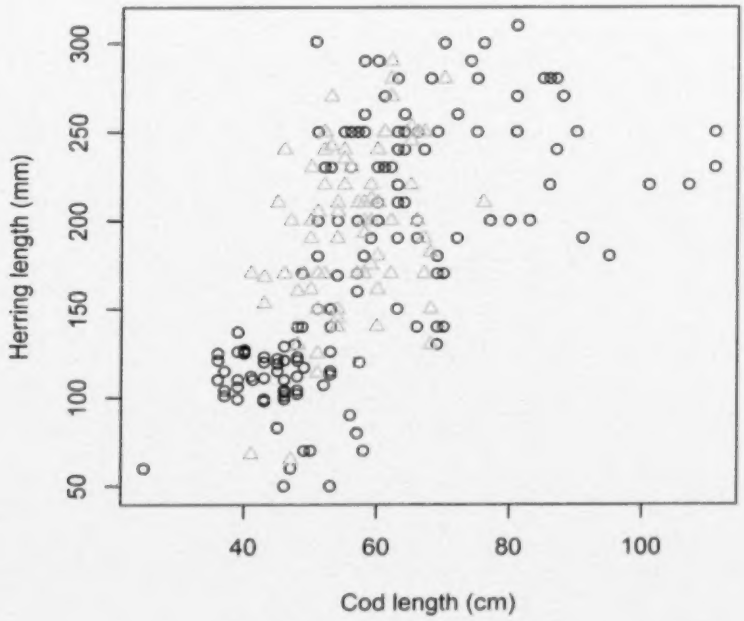

Figure 13. Relationship between Cod predator lengths and Herring prey lengths for samples taken from 1987 to 2002 (black circles; Hanson and Chouinard, 2002) and from 2004 to 2013 (grey triangles; H. Benoît, Fisheries and Oceans Canada, unpublished data).

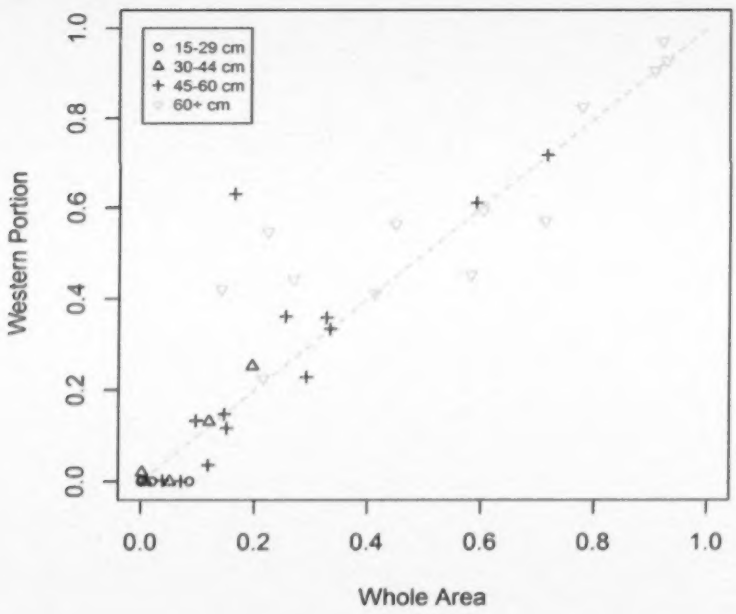

Figure 14. Estimates of average proportion of Herring in the diet of Cod in four size groups based on sampling conducted throughout the sGSL (x-axis, whole area) and sampling restricted to the western portion of the sGSL (y-axis, western portion) defined as the area west of 63° longitude. Each point represents an annual estimate.

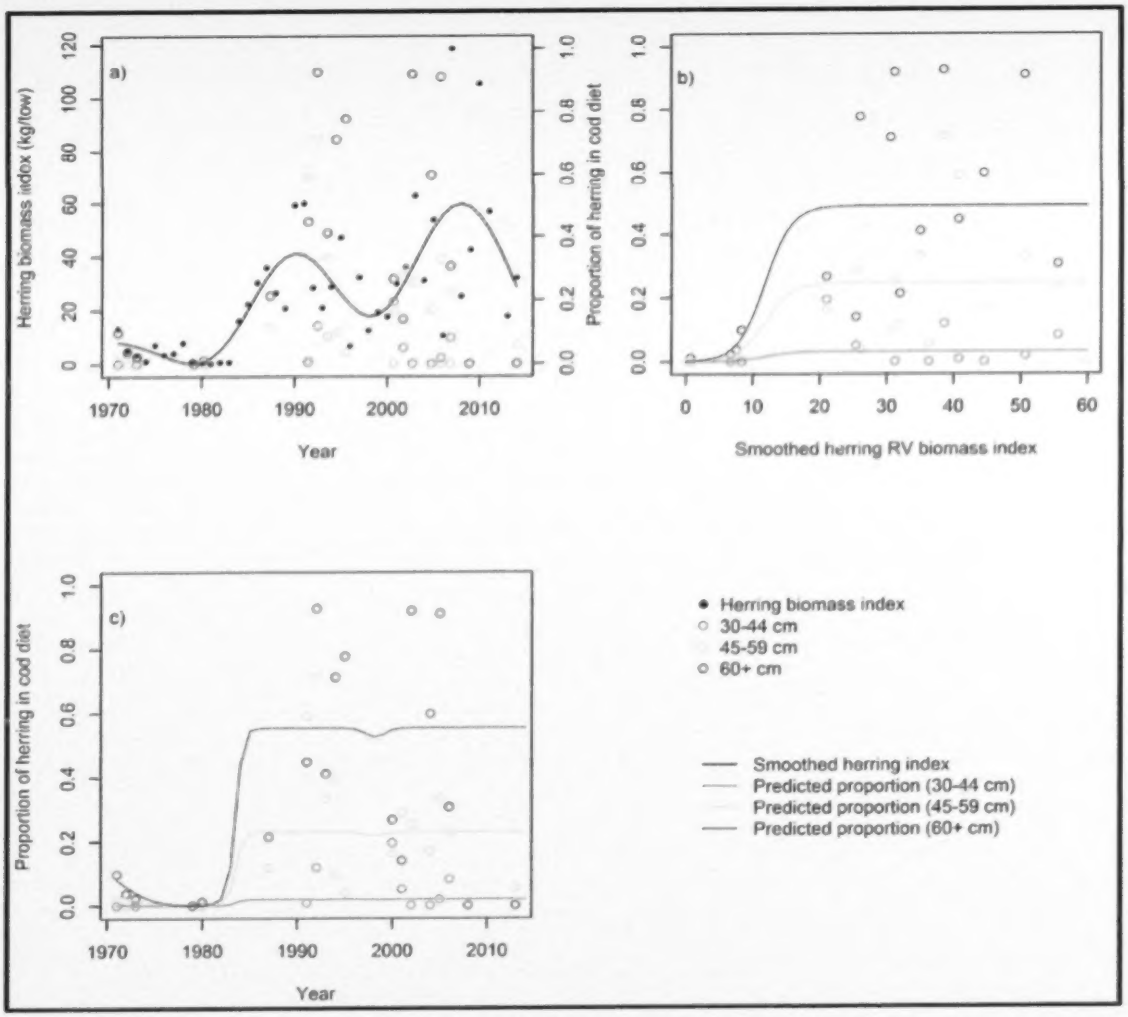

Figure 15. Patterns in the average proportion of Herring in the diet of three size groups of Cod during late summer. Panel a (top left): proportion in the diet (secondary y-axis) and biomass index for sGSL Herring from the September research vessel survey (primary y-axis; black points are the stratified mean estimates and the black line is the smoothed index based on a GAM with 8 degrees of freedom), both as a function of year. Panle b (top right): proportion in the diets as a function of the smoothed Herring abundance index, with coloured lines showing the fit of the functional response model relating diet proportion to Herring abundance. Panel c (bottom left): proportion in the diets as a function of year, with coloured lines showing the predicted proportions based on the functional response model.

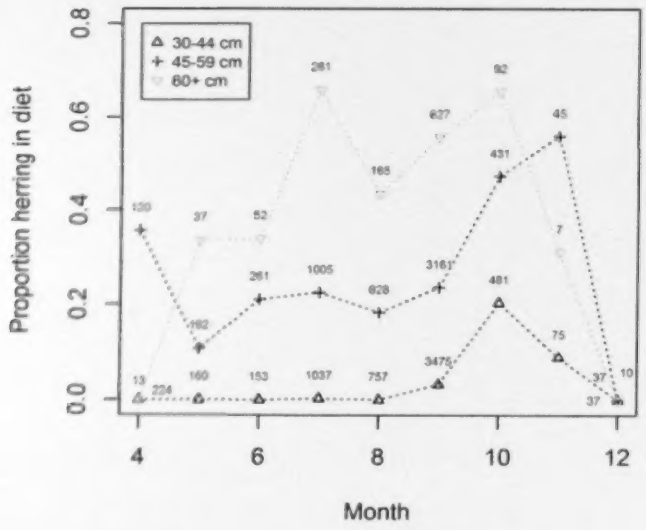

Figure 16. Average proportion of Herring in the diet of three size groups of Cod as a function of month, based on sampling from 1990 to 2013. The number of food-bearing stomachs examined are indicated for each estimate.

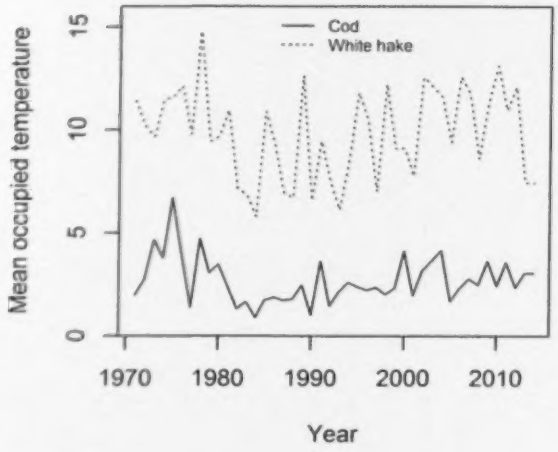

Figure 17. Annual patterns in the mean abundance-weighted temperatures (°C) occupied by Cod ≥ 30cm and White Hake ≥ 25 cm in the annual September research vessel survey. For White Hake, the estimates are restricted to fish in near and mid-shore strata, which is the area in which they feed on Herring.

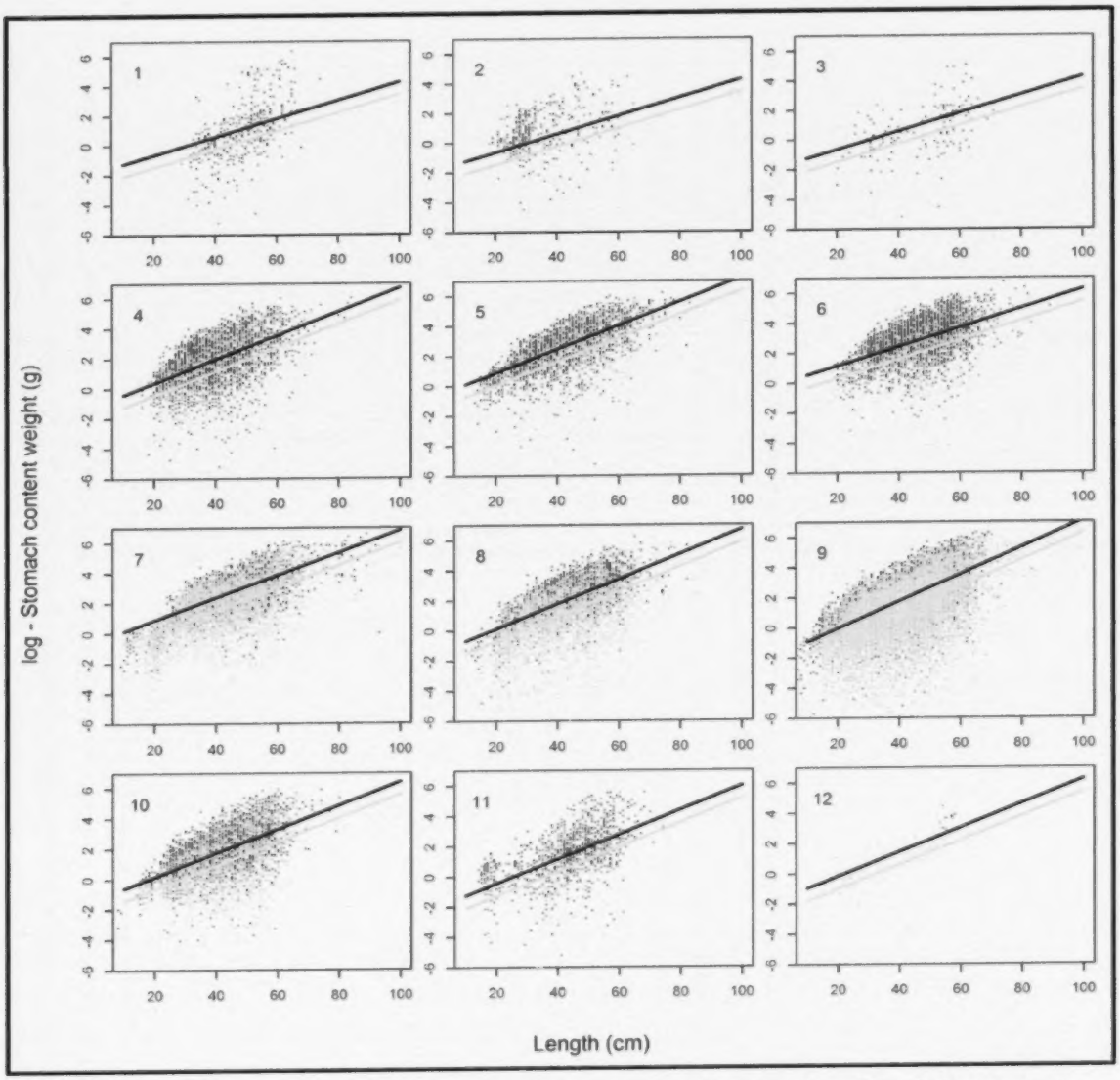

*Figure 18. Cod stomach content weight (in grams; log-tranformed) as a function of length (cm; x-axes) and month (panels) based on observations from Cod-condition sampling (black points) and observed total prey weights (grey points). The lines represent the predictions from the analysis of covariance model of the form log(Stomach Weight) ~ Source + Month + Length + Month*Length, where source is either Cod-condition sampling or observed prey weights.*

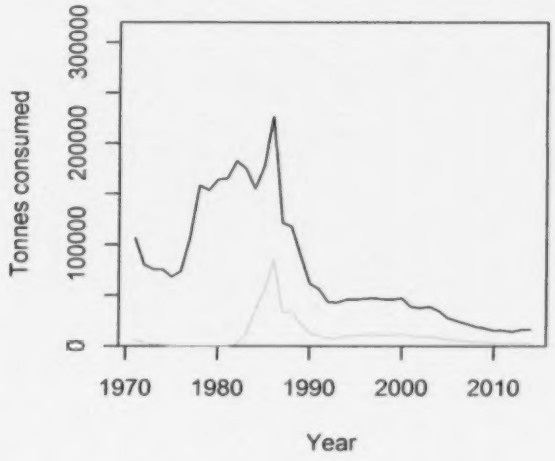

Figure 19. Estimated trends in the annual consumption of all prey (black line) and Atlantic Herring specifically (grey line) by sGSL Cod aged 2 years and older.

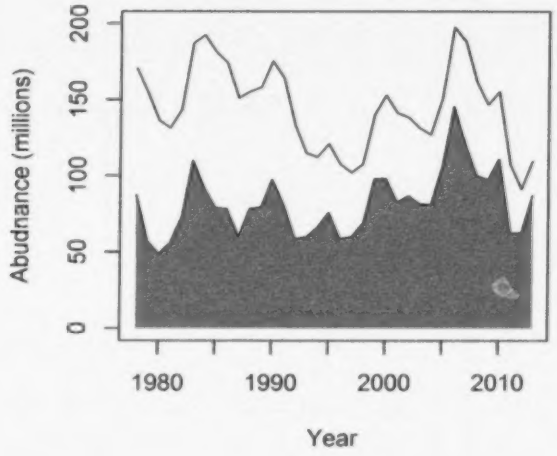

Figure 20. Abundance of sGSL White Hake based on statistical catch-at-age modelling (Swain et al. 2015c). The shaded area represents the abundance of two year old White Hake, while the white area represents the abundance of White Hake three years and older.

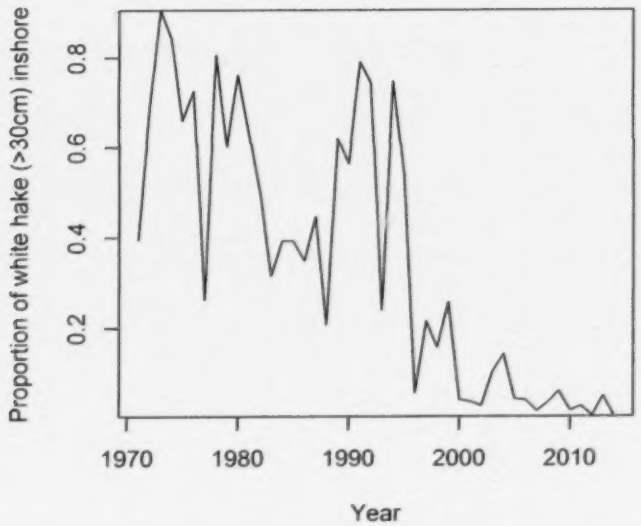

Figure 21. Trends in the proportion of White Hake larger than 30 cm occurring in near and mid-shore strata during the annual September research vessel survey of the sGSL.

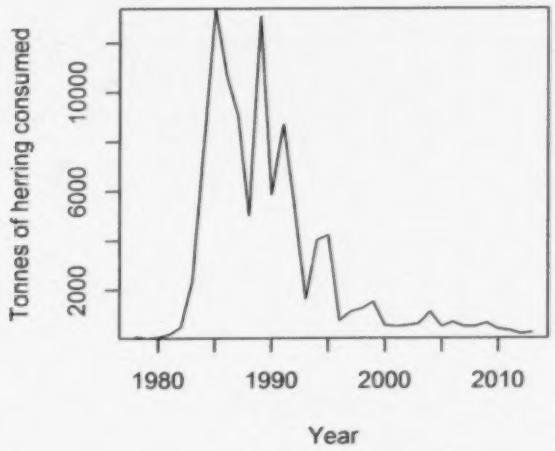

Figure 22. Estimated trends in the annual consumption of Atlantic Herring by sGSL White Hake aged 2 years and older.

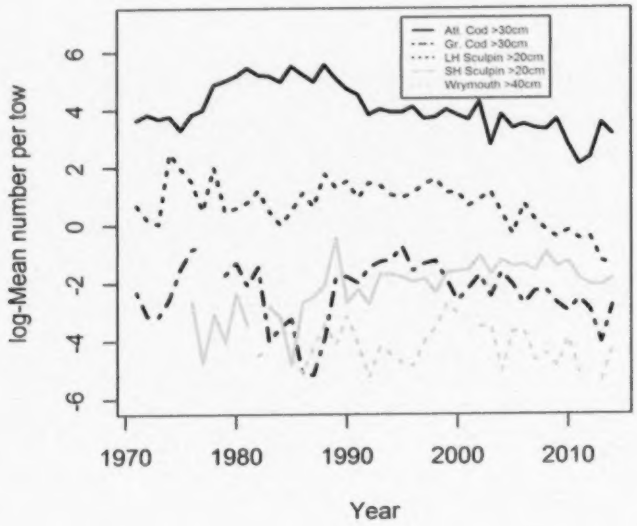

Figure 23. Relative abundance indices (log-mean number per tow) from the September research vessel survey of known species and sizes of groundfish predators of Atlantic Herring.

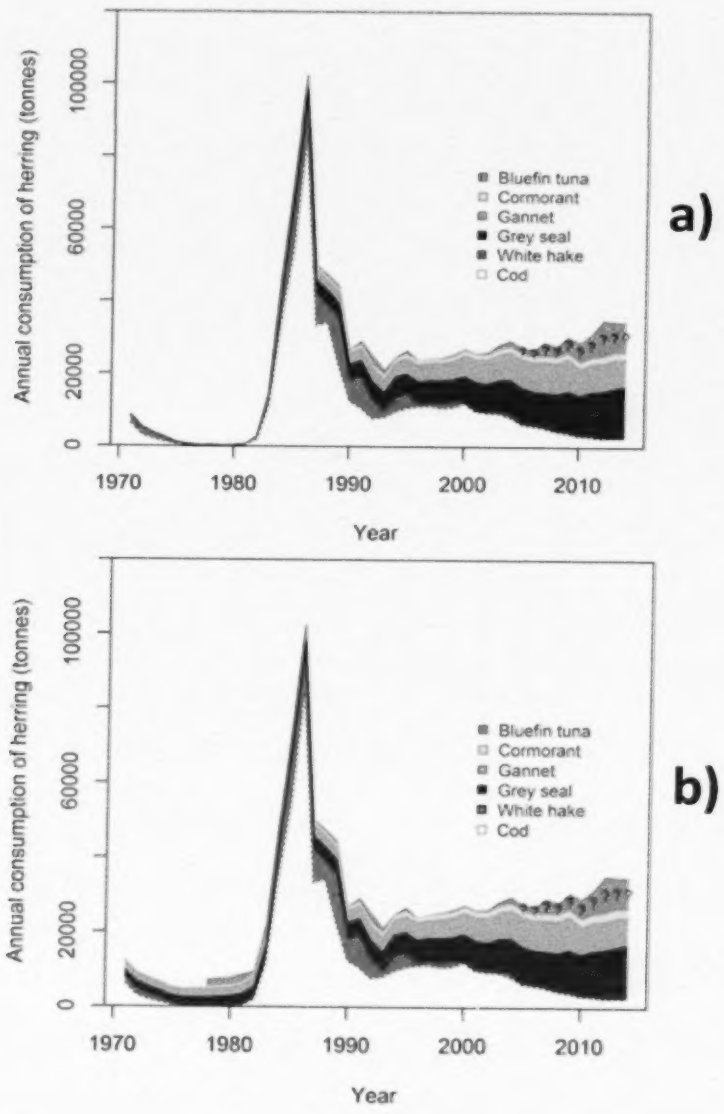

Figure 24. Estimated consumption of late juvenile and adult sGSL Herring by non-cetacean predators. In panel (a), the estimates are based on the assumption that the amount of Atlantic Herring in each predator's diet varied as a function of Herring abundance. In panel (b), the estimates assume no change in diet composition for all predators except Atlantic Cod. The consumption estimates for Bluefin Tuna are indicated with question marks (?) to recall that there is much uncertainty about the abundance of this predator in the sGSL. Note that estimates for Bluefin Tuna begin in 1978.